
Volume 89
Number 1
2002

Annals
of the
Missouri
Botanical
Garden



A SYSTEMATIC REVISION OF *Breonia* (RUBIACEAE–
NAUCLEEAE)¹ Sylvain G. Razafimandimbison^{2,3}

ABSTRACT

Breonia A. Rich., a Malagasy endemic genus of the tribe Naucleae (Rubiaceae, Cinchonoideae), is revised here. The morphology of *Breonia* species is described and compared with that of the other Malagasy Naucleae, *Breonadia* Ridsdale, *Gyrostipula* J.-F. Leroy, and *Janotia* J.-F. Leroy. *Breonia* is distinguished from these genera by having flattened and elongated placentae, imbricate ovules, and indehiscent, multiple fruits rather than triangular placentae, ovules attached side by side to the base of the placentae, and free, capsular fruits as in these genera. *Neobreonia* Ridsdale is again included in *Breonia*. Twenty species are recognized, including eight that are new to science. A full taxonomic treatment, keys, and distribution maps of the recognized species are provided. The newly described species are illustrated.

Key words: accrescent disk, *Breonia*, Cinchonoideae, floral nectary, Madagascar, Naucleae, Rubiaceae.

Breonia A. Rich. is a Malagasy endemic genus of the tribe Naucleae (Cinchonoideae, Rubiaceae) and is the most diverse member of Naucleae there. Species of *Breonia* are large trees, or rarely shrubs, that occupy habitats ranging from eastern rainforests to western deciduous dry forests as well as

swampy forests; they are absent from the semi-arid regions of southern Madagascar. The present revision recognizes 20 species within *Breonia*, of which 8 are newly described herein. *Breonia* is distinguished from the other Malagasy Naucleae, *Breonadia* Ridsdale, *Gyrostipula* J.-F. Leroy, and *Janotia*

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J.-F. Leroy, by having flattened, elongated placentae, imbricate ovules, and indehiscent, multiple fruits rather than triangular placentae, ovules attached side by side to the base of the placentae, and free, capsular fruits as in these genera. Evidence from recent molecular studies (Razafimandimbison & Bremer, 2002) showed that the monotypic genus *Neobreonia* Ridsdale and *Breonia* sensu Ridsdale together formed a monophyletic group. A more recent phylogenetic study by Razafimandimbison and Bremer (in prep.) based on four data sets (ITS, *rbcL*, *trnT-L-F*, and morphological) placed *Neobreonia* within *Breonia*, making the latter paraphyletic. Both genera have multiple fruits and large accrescent disks. In light of this evidence, I here merge *Neobreonia* with *Breonia*. Both studies also showed that *Breonia* is more closely related to *Breonadia*, *Gyrostipula*, and *Janotia* than it is to the rest of Naucleaeae.

Recognition of *Breonia* as a separate genus is widely accepted (e.g., Ridsdale, 1975). However, its circumscription and species limits have been controversial (Haviland, 1897; Homolle, 1938; Ridsdale, 1975). Many more specimens were available for the present study than for earlier studies. Ridsdale's revision was based primarily on the specimens of *Breonia* in the Paris herbarium (P). However, many of the specimens from the Forestry herbarium in Madagascar (TEF) studied here are not held as duplicates in P. Therefore, Ridsdale did not see them.

MATERIALS AND METHODS

This revision is based on the examination of over 260 herbarium specimens and on field observations of 9 of the 20 *Breonia* species. Specimens from the following herbaria were examined and annotated during this study: BR, K, L, MO, P, PRE, TAN, and TEF (see Appendix 1). All specimens with "SF" meaning "Station Forestière," and "RN" meaning "Réserves Naturelles," were collected by Malagasy technicians under the supervision of the French botanist René Capuron. I used the "SF" and "RN" numbers rather than the collector numbers because many specimens of this series do not have collector names on their labels. Also, these are the numbers used in the TROPICOS database of the Missouri Botanical Garden.

Fieldwork was conducted in Madagascar in May–July of 1995 and 1996, respectively, and January–June of 1998 to collect herbarium specimens and pickled material of *Breonia* species, as well as to gather ecogeographical data. The pickled material was preserved in formalin/acetic acid/ethanol,

Table 1. Distinctive fertile morphological features separating *Breonia* and *Sarcocephalus*.

Characters	<i>Breonia</i>	<i>Sarcocephalus</i>
Inflorescence position	axillary	terminal
Involucral bract	always surrounding the young inflorescence	never surrounding the young inflorescence
Attachment of placentae to septa	to the septal apices	to the middle of the septa
Stigma shape	globose, clavate, capitate	spindle-shaped
Receptive areas on the stigmatic lobe	ca. apical	ca. basal
Accrescent disks	present	absent
Number of ovules per locule	1 to 9	more than 50

FAA (Radford et al., 1973). This allowed detailed studies of inflorescences and infructescences and revealed a number of important characters, which are impossible to observe in dried specimens.

TAXONOMIC HISTORY

IDENTITY OF *BREONIA*

Breonia was originally described by Achille Richard (De Candolle, Sep. 1830); he named the genus after the early 19th century French botanist Jean Nicolas Bréon, one of the first collectors. In 1879, Baillon placed *Breonia* in the synonymy of *Sarcocephalus* Afz. ex Sabine solely because both have multiple fruits, a character that evolved at least three times in Naucleaeae (Razafimandimbison & Bremer, 2002). Baillon included two species of *Sarcocephalus*, *S. madagascariensis* (A. Rich.) Baill. and *S. richardiana* Baill., from Madagascar. *Breonia* is quite distinct from *Sarcocephalus* in many aspects (see Table 1). Schumann (1891), Haviland (1897), and Homolle (1938) all endorsed the recognition of *Breonia* as a separate genus. The separation of *Breonia* and *Sarcocephalus* and the monophyly of *Breonia* is strongly supported by ITS and *rbcL* sequence data (Razafimandimbison & Bremer, 2002).

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Table 2. Species circumscriptions of *Breonia*.

Haviland (1897)	Homolle (1938)	Ridsdale (1975)	Razafimandimbison (2001)
<i>boivinii</i>	<i>boivinii</i>	<i>boivinii</i>	<i>boivinii</i>
<i>coriacea</i>	— ¹	not mentioned	— ⁴
<i>cuspidata</i>	<i>cuspidata</i>	— ³	<i>cuspidata</i>
<i>longipetiolata</i>	dubious species	dubious species	dubious species
<i>madagascariensis</i>	<i>madagascariensis</i>	<i>madagascariensis</i>	<i>madagascariensis</i>
<i>mauritiana</i>	— ¹	— ³	— ⁴
<i>membranacea</i>	<i>membranacea</i>	— ³	<i>membranacea</i>
<i>parvifolia</i>	<i>parvifolia</i>	<i>sphaerantha</i>	<i>sphaerantha</i>
<i>richardiana</i>	<i>richardiana</i>	— ³	— ⁴
<i>stipulata</i>	— ¹	— ³	<i>stipulata</i>
	<i>decaryana</i>	<i>Neobreonia decaryana</i>	<i>decaryana</i>
	<i>havilandiana</i>	— ³	<i>havilandiana</i>
	<i>keliravina</i>	— ⁵	— ⁵
	<i>lowelii</i>	— ³	<i>lowelii</i>
	<i>macrocarpa</i>	— ²	<i>macrocarpa</i>
	<i>perrieri</i>	<i>perrieri</i>	<i>perrieri</i>
		<i>citrifolia</i>	<i>chinensis</i>
			<i>capuronii</i>
			<i>fragifera</i>
			<i>lowryi</i>
			<i>richardsonii</i>
			<i>sambiranensis</i>
		— ³	<i>taolagnaroensis</i>
			<i>tayloriana</i>
			<i>tsaratananensis</i>

—¹ merged in *B. richardiana*; —² merged in *B. madagascariensis*; —³ merged in *B. citrifolia*; —⁴ merged in *B. chinensis*; —⁵ merged in *B. decaryana*.

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PREVIOUS SPECIES DELIMITATION IN *BREONIA*

The species limits used by previous authors have been controversial. Haviland (1897), in his first worldwide revision of the tribe Naucleae, recognized 10 species of *Breonia* (Table 2). He used petiole length and secondary leaf vein number to divide the genus into two major groups: the first group

comprising *Breonia madagascariensis*, with subsessile leaves and 12 secondary veins (there are actually 18 or 19 secondary veins, but the leaf blade of the type specimen is folded, so Haviland must have counted what he could see); and the second group containing the remaining species, which had petiolate leaves with 9 to 11 secondary veins. Haviland then used leaf blade length and width, as well as inflorescence width, to delimit the species of his second "petiolate" group. Forty years later, Homolle (1938) adopted new species circumscriptions for *Breonia*. She retained six species from Haviland's treatment, but also described six new species (see Table 2). Unfortunately, she did not provide a key to the species she recognized. Ridsdale (1975) proposed new circumscriptions for *Breonia* based on a combination of the following characters: stipules of terminal vegetative buds conical and obovulate; inflorescences always lateral; calyptra-like bracts coherent, surrounding the young inflorescence, and circumscissile; adjacent calyx tubes free and persistent; calyx lobes densely pubescent; and placentae attached to the upper third of the septum. He used the shape and length of stipules of terminal vegetative buds, the mature stipule length,

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and the leaf shape and size as primary characters and recognized only five species (Table 2). He placed *Breonia decaryana* Homolle and *B. keliravina* Homolle in his new genus *Neobreonia* because of their partly fused calyx tubes and complanate terminal vegetative buds.

Capuron (1973a), in an unpublished manuscript deposited at P, recognized 13 species using variation in leaf blade size, stipule shape and length, calyx tube length and indumentum, ovule number, and fruit surface. However, he provided neither descriptions of the new species that he recognized nor a key for their identification.

ON THE IDENTITY OF *CEPHALANTHUS CHINENSIS* LAM.
AND *ANTHOCEPHALUS* A. RICH.

This section presents the problem of the identity of *Cephalanthus chinensis* Lam. [= *Breonia chinensis* (Lam.) Capuron] and its historical confusion with *Breonia*. This issue has caused a long and controversial debate during the last 30 years (cf. Bakhuizen van den Brink, 1970; Capuron, 1973b; Ridsdale, 1975; Bosser, 1984, 1999).

Lamarck (1785: 678) claimed that a specimen he received from Sonnerat was the type of his *Cephalanthus chinensis*. On the other hand, Richard (Sep. 1830) also stated that he described his *Anthocephalus* [= *Neolamarckia* Bosser] as an Asian, and not Malagasy, monotypic genus (*Anthocephalus indicus*) based on specimens labeled "*C. chinensis* Lam." Lamarck and Richard gave no further details about their type specimens. Bakhuizen van den Brink (1970) and Ridsdale (1975) surmized that the collection of Sonnerat that served as the type of *C. chinensis* was also used by Richard to describe his *Anthocephalus*. Capuron (1973b) and Bosser (1984, 1999) argued that *C. chinensis* Lam. and *Anthocephalus* A. Rich. were not necessarily based on the same specimen.

In the Lamarck herbarium in Paris (P-LA) there is an authentic specimen of *Cephalanthus* with five different labels attached to it. The first label is Lamarck's and says "*Cephalanthus chinensis* enc n° 2." The second label is in Commerson's handwriting (Bosser, 1984), with a short Latin description and the country of origin mentioned as "Isle de France" (i.e., Mauritius). The third label is Sonnerat's and says "c'est la *Morinda* de Chine." The fourth label is also Sonnerat's, on which he wrote "*Morinda* de Chine," and below this name Lamarck added "*Cephalanthus*." The fifth label was written by Roeper and says "*Nauclea purpurea* Roxb." and "*Nauclea orientalis* Lam." This specimen sheet was considered by Capuron (1973b) and Bosser (1984, 1999)

to be the type of Lamarck's *Cephalanthus chinensis*. However, Bakhuizen van den Brink (1970) and Ridsdale (1975) disagreed because this specimen does not match Richard's description of *Anthocephalus*. Despite the fact that no one has ever found a collection of Sonnerat *s.n.* in P or P-LA that could have served as the type of both *C. chinensis* Lam. and *Anthocephalus*, Bakhuizen van den Brink and Ridsdale inferred that Lamarck must have based his *C. chinensis* on such a collection. This collection, they further surmized, must contain two elements, one of *Breonia* and the other of *Anthocephalus*. They also argued that Richard must have typified his *Anthocephalus indicus* by only the element of *Anthocephalus* of this hypothetical Sonnerat collection. Bakhuizen van den Brink then typified *Anthocephalus* by only the element of *A. indicus* of this hypothetical Sonnerat collection, excluding its element of *Breonia*. Ridsdale (1975) endorsed Bakhuizen van den Brink's arguments and chose the unverified or non-existent collection as the lectotype of *Anthocephalus*.

Capuron (1973b), followed by Bosser (1984, 1999), disagreed with Bakhuizen van den Brink (1970) and Ridsdale (1975). Capuron and Bosser argued that the type specimen of *Cephalanthus chinensis* Lam. was the specimen with five labels in P-LA because the original description of *C. chinensis* Lam. (Lamarck, 1785: 678) matches this plant, and Lamarck himself annotated it. Bosser argued that Lamarck was apparently influenced by Sonnerat's labels stating "*Morinda* de Chine," and assumed that the plant originally grew in China, the Philippines, and the Moluccas (Bosser, 1984: 244). Bosser then inferred that Sonnerat's label meant that Sonnerat had seen the specimen of *C. chinensis* now in P-LA, and that it reminded him of what he called "*Morinda* de Chine." Bosser (1984) also argued that the second label was Commerson's because there is a similar specimen in P labeled *C. chinensis* Lam. and it was collected by Commerson in Mauritius. In addition, the specimen with five labels in P-LA shows axillary inflorescences and adjacent flowers with fused ovaries that are characteristic of *Breonia*. Capuron (1973b) then concluded that *C. chinensis* Lam. was based on a plant originally from Madagascar rather than Asia, and therefore belongs to *Breonia*. Consequently, Capuron made the new combination *B. chinensis* (Lam.) Capuron.

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and the leaf shape and size as primary characters and recognized only five species (Table 2). He placed *Breonia decaryana* Homolle and *B. keliravina* Homolle in his new genus *Neobreonia* because of their partly fused calyx tubes and complanate terminal vegetative buds.

Capuron (1973a), in an unpublished manuscript deposited at P, recognized 13 species using variation in leaf blade size, stipule shape and length, calyx tube length and indumentum, ovule number, and fruit surface. However, he provided neither descriptions of the new species that he recognized nor a key for their identification.

ON THE IDENTITY OF *CEPHALANTHUS CHINENSIS* LAM.
AND *ANTHOCEPHALUS* A. RICH.

This section presents the problem of the identity of *Cephalanthus chinensis* Lam. [= *Breonia chinensis* (Lam.) Capuron] and its historical confusion with *Breonia*. This issue has caused a long and controversial debate during the last 30 years (cf. Bakhuizen van den Brink, 1970; Capuron, 1973b; Ridsdale, 1975; Bosser, 1984, 1999).

Lamarck (1785: 678) claimed that a specimen he received from Sonnerat was the type of his *Cephalanthus chinensis*. On the other hand, Richard (Sep. 1830) also stated that he described his *Anthocephalus* [= *Neolamarckia* Bosser] as an Asian, and not Malagasy, monotypic genus (*Anthocephalus indicus*) based on specimens labeled "*C. chinensis* Lam." Lamarck and Richard gave no further details about their type specimens. Bakhuizen van den Brink (1970) and Ridsdale (1975) surmized that the collection of Sonnerat that served as the type of *C. chinensis* was also used by Richard to describe his *Anthocephalus*. Capuron (1973b) and Bosser (1984, 1999) argued that *C. chinensis* Lam. and *Anthocephalus* A. Rich. were not necessarily based on the same specimen.

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Bosser (1984) has pointed out correctly that our problem is to find out whether the specimen of *C. chinensis* in P-LA conformed to what Lamarck said in his original description of *C. chinensis*, rather than what Richard said about *Anthocephalus*. Indeed, Bosser argued that Richard may not have seen the specimen of *C. chinensis* in P-LA because Lamarck sold his herbarium to Roeper in 1824 and the entire collection was not returned to Paris until 1886, while Richard's work was in press for publication in 1830. Richard's original description of *Anthocephalus* indicates that he used specimens with flowers and fruit, whereas Lamarck had a specimen with flowers only; therefore, even if Richard had seen the specimen in P-LA, he would still have needed a specimen with fruit. Finally, *Anthocephalus*, as Richard noted, has terminal inflorescences, whereas the specimen of *C. chinensis* in P-LA has axillary inflorescences. Therefore, Bakhuizen van den Brink's and Ridsdale's scenarios of *C. chinensis* being based on mixed elements of *Breonia* of Sonnerat and *Anthocephalus* is untenable, in agreement with Bosser (1999).

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SPECIES CIRCUMSCRIPTIONS IN *BREONIA* SENSU RAZAFIM.

Haviland's (1897) circumscription of *Breonia* species based on secondary leaf veins, leaf blades, and inflorescences is problematic because these characters overlap for some well-defined species. Using such features as stipules of terminal vegetative bud size, mature stipule length, and leaf shape and size as primary discriminating characters forced Ridsdale to lump taxa and recognize only five species, of which three (*Breonia citrifolia*, *B. madagascariensis*, and *B. sphaerantha*) become rather heterogeneous. Neither Haviland (1897) nor Ridsdale (1975) used floral and fruit characters for their keys for *Breonia*. However, there are a number of useful taxonomic characters, such as shapes of the stipules of the terminal vegetative bud and inflorescence axis, corolla lobe indumentum, the degree of fusion of adjacent ovaries, accrescent disks, and infructescence surfaces. As a result, I abandon Haviland's (1897) and Ridsdale's (1975) species delimitations and adopt here new species limits within *Breonia*.

My criterion for recognizing species is the presence of one or more apparently fixed or non-overlapping morphological differences between putative species. Morphologically distinct groups of specimens were identified and delimited by non-overlapping or fixed diagnostic differences; these diagnosable morphological units, which I refer to as species, are hypotheses until new data are available to refute them. To relate this functional species concept to more theoretical ones, one must test it on the basis of the criteria defining each theoretical species concept.

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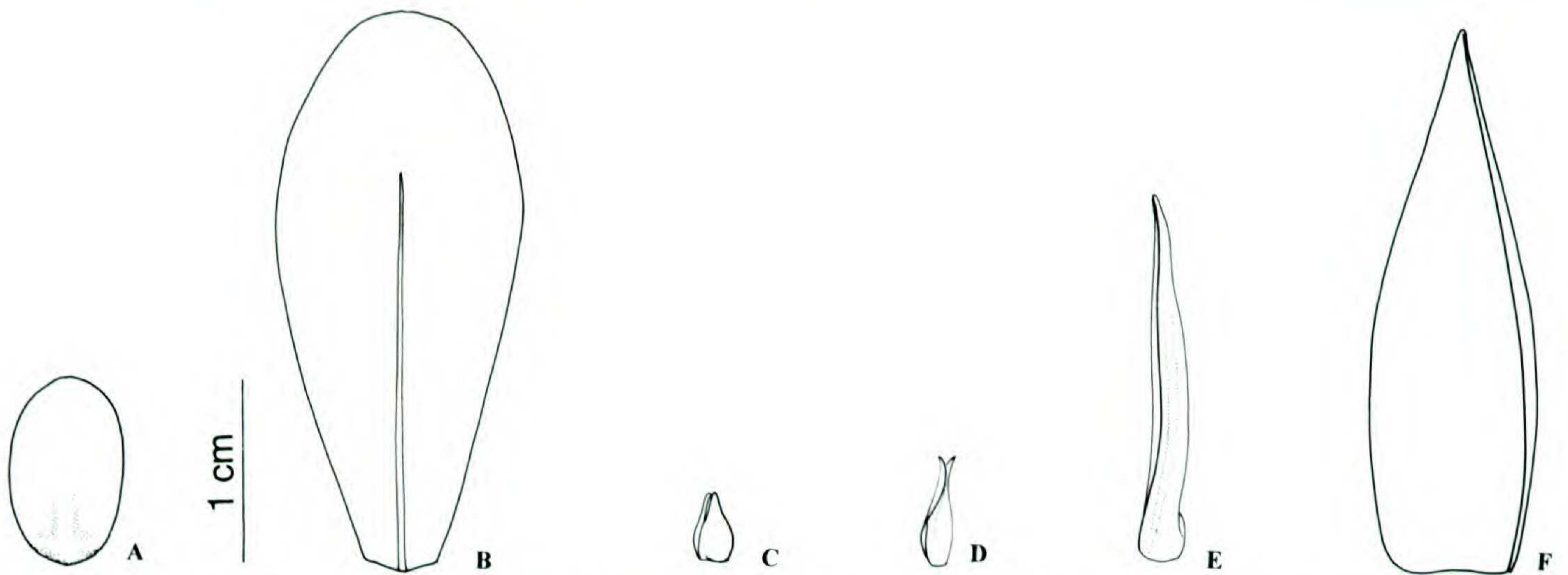


Figure 1. Variation in shape and size of the stipules of the vegetative buds in *Breonia* (A, C–F) and *Janotia*.—A *Breonia decaryana*.—B. *Janotia macrostipula*.—C. *B. capuronii*.—D. *B. chinensis*.—E. *B. stipulata*.—F. *B. madagascariensis*.

MORPHOLOGY AND TAXONOMIC CHARACTERS OF *BREONIA*

A detailed overview of the morphological characters of *Breonia* species is presented as well as their taxonomic significance. The allied Malagasy genera *Breonadia*, *Gyrostipula*, and *Janotia* are also discussed for comparison.

HABIT

Plants of *Breonia* are medium to large, sometimes emergent trees up to 30 m tall, rarely shrubs. Buttresses are reported in *Breonia sphaerantha*. The bark is smooth to rugose. The trunk is typically straight. The branches are usually plagiotropic.

LEAVES

Breonia leaves are simple, opposite, and decussate, as in most Rubiaceae, and generally coriaceous to membranaceous. The length of petioles and the size of leaf blades are useful for recognizing some species. The leaves of *Breonia* are petiolate or rarely sessile (*B. madagascariensis*). Most species have small to medium-sized leaves, but two species (*B. macrocarpa* and *B. madagascariensis*) have relatively large leaf blades: the former to 38 × 25 cm, and the latter up to 45 × 35 cm. The leaf blades are mostly glabrous, or rarely pubescent in a few individuals of *B. perrieri*. *Breonia macrocarpa* is characterized by having brown, long hairs on the lower surface of the leaf blades.

Domatia. Domatia are cavities located in the axils of veins on the abaxial sides of leaf blades (Jacobs, 1966). They typically occur in the axils of secondary veins in most species of *Breonia*. Mites or mite eggs can be found in the domatia, although the occurrence of domatia is not dependent on the

arachnid presence; these domatia may provide the host plant protection from herbivores or pathogens (Pemberton & Turner, 1989). The type and location of domatia are useful for species delimitation in *Breonia*. In *B. macrocarpa*, they occur in the axils of the secondary and tertiary veins. Both secondary and tertiary domatia have never been seen in other Naucleaceae; they are only known in a few members of Rubiaceae (e.g., *Aoranthe*, *Pleiocoryne*, *Oligocodon*) (Robbrecht, 1988). In *Breonia*, domatia can be tufts (covered by dense hairs), or cryptic and glabrous, or pits (depressions in the lamina with a broad opening).

Venation. The venation of the leaf blades is usually prominulous on the upper sides of the leaf blades, but is prominent in *Breonia havilandiana*, *B. madagascariensis*, and *B. tsaratananensis*. The secondary venation is usually eucamptodromous (Radford et al., 1973).

Stipules of terminal vegetative buds. The stipules of terminal vegetative buds are usually conical and obvolute in most *Breonia* species (Fig. 1C–F). In these, two stipules overlap in the bud such that one half of each is external and the other half is internal (Harris & Harris, 1994). Their sizes and lengths vary between species, which is useful for their identification. In *Breonia decaryana* and *Janotia macrostipula*, the stipules of terminal vegetative buds are complanate (Fig. 1A, B), the two stipules being flat and pressed together. In *Gyrostipula*, they are long, filiform, and convolute, one stipule being rolled inside another (Radford et al., 1973).

Mature stipules. The stipules of *Breonia* and other Malagasy Naucleaceae are interpetiolar, boat-shaped (cymbiform), and usually abaxially carinate. The keels are prominulous in many species and prominent in *B. tayloriana* and *B. madagascariensis*.

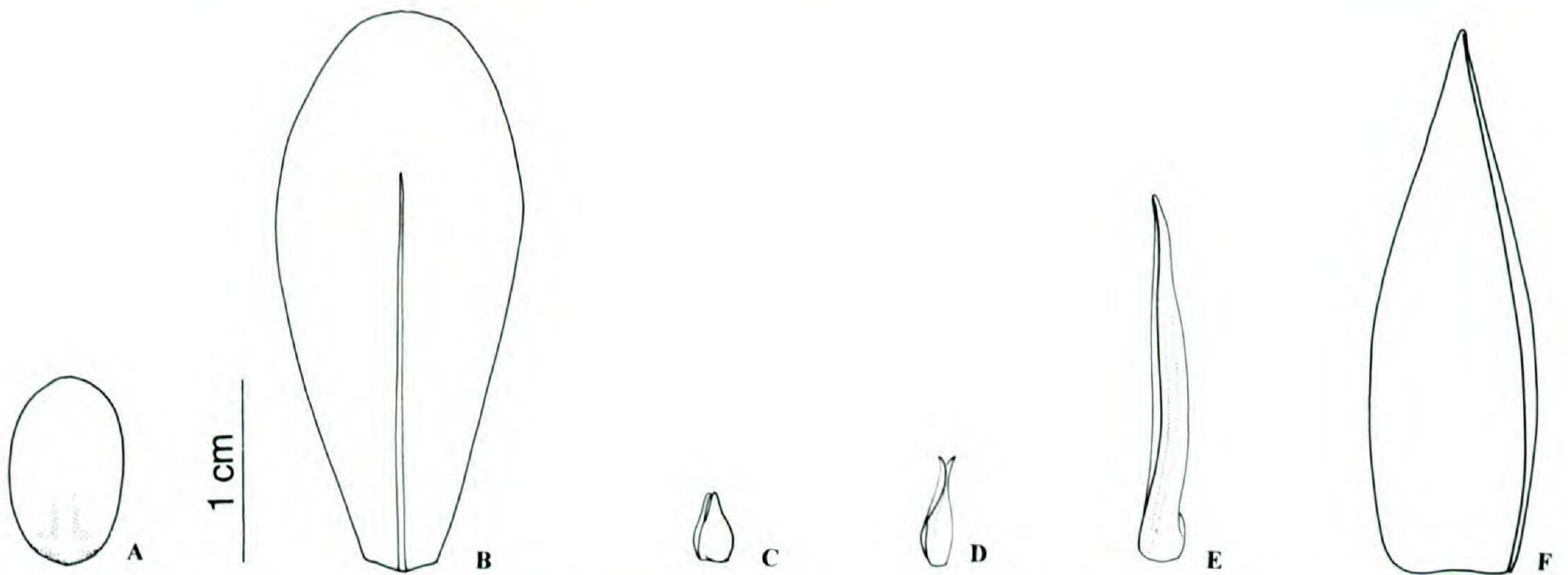


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sis. In *Gyrostipula*, the stipules are without keels and are twisted when dry. The size and persistence of the stipules vary among species of *Breonia* and are useful for species distinction. Stipules are typically deciduous in *Breonia*. In *Breonia tayloriana*, they are semi-persistent.

INFLORESCENCES

Like other Naucleaeae, *Breonia* species have globose inflorescences on which numerous small flowers (usually more than 50) form dense clusters rather than capitate inflorescences found in other Rubiaceae (e.g., Schradereae, Psychotrieae). The individual flowers are inconspicuous, and the entire cluster of flowers acts as a single attractive unit.

Inflorescence stalk. In *Breonia*, the inflorescence stalk is typically articulate and composed of a peduncle, a node, and an inflorescence axis (e.g., Figs. 6F, 9E, 14C). Ridsdale (1975) used the term "flowering axes" to refer to what I call inflorescence axes; he called "true peduncles" what I refer to as peduncles. An evident node separates the peduncle from the inflorescence axis. The inflorescence axis is located between the branch bearing the inflorescence and the node. The peduncle is located between the node and the base of the head; this is hidden by the bracts prior to the separation of the bract lobes. The peduncle can be absent (e.g., Figs. 15A, 16F); in some species (e.g., Fig. 6F, *Breonia capuronii*; *B. decaryana*), this continues to elongate after the inflorescence axis has finished growing at the end of anthesis. The length and shape of the inflorescence axes are useful for recognizing species in *Breonia*. Inflorescence axis shapes can be terete (e.g., *Breonia capuronii*, *B. perrieri*, *B. richardsonii*, *B. sphaerantha*) or flattened (e.g., *B. chinensis*, *B. havilandiana*, *B. membranacea*, *B. stipulata*, and *B. tayloriana*). The inflorescence axes are usually longer than the peduncles; however, in *Breonia decaryana*, *B. capuronii*, and *B. sphaerantha*, the two are similar in size and shape.

Bracts. Most *Breonia* species have bracts that are coherent, but histologically distinct (Radford et al., 1973), valvate, and completely enclose the young inflorescence in a calyptra-like fashion. As the inflorescences develop, the bracts separate longitudinally into two lobes on the nodes lasting for only a few days and usually falling off before anthesis. They may persist for two or three weeks after anthesis in *Breonadia*, *Gyrostipula*, and *Breonia decaryana*. In *B. richardsonii*, the bracts are tubular, appressed to the inflorescence axis, and terminated by three to four broadly triangular lobes. They never enclose the young inflorescence. This is unique

in *Breonia* and the whole of Naucleaeae. Finally, the bracts in *Breonia* are usually glabrous, except in *B. macrocarpa* and *B. tsaratananensis*, where they are densely pubescent. The position of the bract varies depending on whether or not the peduncle continues to elongate after the inflorescence axis ends its elongation. When the peduncle does not elongate, the bract lies immediately below the inflorescence, as in *B. chinensis*, *B. cuspidata*, *B. madagascariensis*, and *B. taolagnaroensis*.

Ridsdale's (1975) descriptions of calyptra-like bracts of *Breonia* being coherent, surrounding the young inflorescence, and circumscissile, appear to be incorrect. I have seen two herbarium specimens of *Breonia chinensis* showing circumscissile calyptra-like bracts. In several species, including *B. chinensis*, *B. havilandiana*, *B. macrocarpa*, *B. membranacea*, and *B. tsaratananensis*, the bracts normally separate longitudinally into two equal hemispheres. This apparent circumscissile rupturing of the bracts evidently happens during specimen preparation. The illustration of *Sarcocephalus richardii* Drake [= *Breonia chinensis* (Lam.) Capuron] in Grandidier (1897: 457) shows the circumscissile calyptra-like rupturing of the bract. It is possible that Ridsdale (1975) was influenced by this illustration.

Interfloral bracteoles are absent in *Breonia*, as well as in *Gyrostipula* and *Janotia*. However, they are present in *Breonadia*. In *Breonia richardsonii* (Fig. 14F), the ovary bases are surrounded by long hairs.

FLOWERS

The flowers in *Breonia* are actinomorphic, hermaphroditic, protandrous, sessile, and usually 5-merous, although 4-merous examples are occasionally encountered. The flowers are typically 4-merous in *B. capuronii*, *B. decaryana*, *B. fragifera*, and *B. sphaerantha*.

Calyx. The calyx tubes (i.e., tubular parts of limb above the hypanthium) in most *Breonia* species are free from each other and clearly visible. In *B. fragifera* and *B. decaryana* the calyces are barely evident. These calyx tubes of adjacent flowers are only partly fused in *B. decaryana*; they are completely fused in *B. fragifera*. Therefore, the degree of calyx fusion is useful for species recognition in *Breonia*.

The shape and surface of the calyx tubes are useful at the species level. In *Breonia chinensis*, *B. lowryi*, *B. tayloriana*, *B. stipulata*, and *B. taolagnaroensis*, the calyx tubes are infundibular and smooth. Other species have infundibular and

sis. In *Gyrostipula*, the stipules are without keels and are twisted when dry. The size and persistence of the stipules vary among species of *Breonia* and are useful for species distinction. Stipules are typically deciduous in *Breonia*. In *Breonia tayloriana*, they are semi-persistent.

INFLORESCENCES

Like other Naucleaeae, *Breonia* species have globose inflorescences on which numerous small flowers (usually more than 50) form dense clusters rather than capitate inflorescences found in other Rubiaceae (e.g., Schradereae, Psychotrieae). The individual flowers are inconspicuous, and the entire cluster of flowers acts as a single attractive unit.

Inflorescence stalk. In *Breonia*, the inflorescence stalk is typically articulate and composed of a peduncle, a node, and an inflorescence axis (e.g., Figs. 6F, 9E, 14C). Ridsdale (1975) used the term "flowering axes" to refer to what I call inflorescence axes; he called "true peduncles" what I refer to as peduncles. An evident node separates the peduncle from the inflorescence axis. The inflorescence axis is located between the branch bearing the inflorescence and the node. The peduncle is located between the node and the base of the head; this is hidden by the bracts prior to the separation of the bract lobes. The peduncle can be absent (e.g., Figs. 15A, 16F); in some species (e.g., Fig. 6F, *Breonia capuronii*; *B. decaryana*), this continues to elongate after the inflorescence axis has finished growing at the end of anthesis. The length and shape of the inflorescence axes are useful for recognizing species in *Breonia*. Inflorescence axis shapes can be terete (e.g., *Breonia capuronii*, *B. perrieri*, *B. richardsonii*, *B. sphaerantha*) or flattened (e.g., *B. chinensis*, *B. havilandiana*, *B. membranacea*, *B. stipulata*, and *B. tayloriana*). The inflorescence axes are usually longer than the peduncles; however, in *Breonia decaryana*, *B. capuronii*, and *B. sphaerantha*, the two are similar in size and shape.

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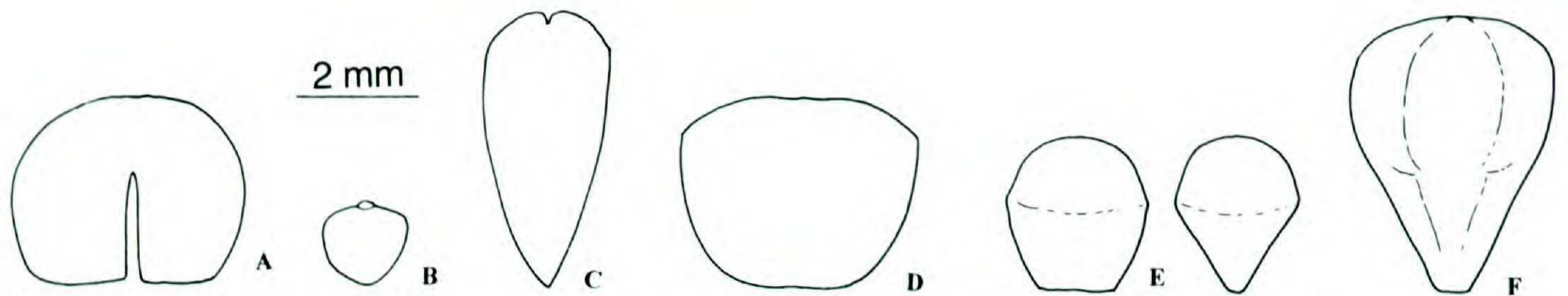


Figure 2. Different shapes of accrescent disks in *Breonia* fruits. —A. *Breonia decaryana*.—B. *B. sphaerantha*.—C. *B. fragifera*.—D. *B. macrocarpa*.—E. *B. chinensis*.—F. *B. taolagnaroensis*.

ribbed calyx tubes. The ribs may be prominulous (e.g., *B. sambiranensis*) or prominent (*B. tsaratananensis* and *B. boivinii*). In *B. tsaratananensis* the calyx tubes are constricted above the middle and narrowed toward the base and the lobes; this is unique in *Breonia*.

The shape of the calyx lobes varies from oblong to triangular, sometimes with truncate apices. *Breonia sambiranensis* has a distinct calyx lobe shape: short, truncate, with a shallow depression in the center and a short appendage on the edge toward the style (Fig. 14D). Broadly triangular and pubescent lobes characterize *Gyrostipula*, while *Breonadia* and *Janotia* have long, linear, pubescent lobes.

Corolla. The corolla of *Breonia* is always hypocrateriform and yellow-tinged. In *B. boivinii*, *B. sambiranensis*, and *B. tsaratananensis*, some of the corolla lobes have dorsal protuberances (e.g., see *B. sambiranensis*, Fig. 14E). Corolla indumentum is useful for species recognition. One species group (*B. chinensis*, *B. cuspidata*, *B. louvelii*, *B. membranacea*, *B. stipulata*, and *B. taolagnaroensis*) has glabrous lobes. *Breonia boivinii*, *B. sambiranensis*, and *B. tsaratananensis* all have pubescent or puberulous lobes. In *B. macrocarpa* and *B. madagascariensis* lobes are puberulous and marginally glabrate.

Nectaries. As in other members of Naucleaeae sensu Razafimandimbison and Bremer (2002), the floral nectaries (i.e., disks) in *Breonia* are inconspicuous, surround the style base, and are embedded in the hypanthia between the base of the corolla tube and the top of the ovary. For all *Breonia*, nectaries continue to grow during infructescence development and become hardened and conspicuous. I call such nectaries “accrescent disks.” Capuron, in his unpublished treatment for Malagasy Rubiaceae at P, also observed this type of disk in *Breonia* but did not understand its nature. These accrescent disks appear to be the single synapomorphy among members of Malagasy Naucleaeae. However, they tend to be much larger in *Breonia* species than in *Breonadia*, *Gyrostipula*, and *Jano-*

tia. The shape of these accrescent disks (Fig. 2) varies from obconical to obtriangular, to pentagonal or rounded. Their shape and size are useful for species distinction. This is the first report of the use of this character in the classification of *Breonia* as well as in Rubiaceae.

Stamens. *Breonia* filaments are usually very short and flattened; they are inserted in the throat of the corolla tubes and sometimes slightly exerted. The anthers are always bicuspid at the base, basifixed, introrse, dehiscing along longitudinal slits.

Gynoeceum. In *Breonia*, ovaries (hypanthia) of individual flowers are always bicarpellate. They are coherent and nonseptate in *Breonia capuronii*, *B. decaryana*, *B. fragifera*, and *B. sphaerantha* (see Figs. 6D, 9F), whereas they are fused (syncarpous) and septate in the remaining species. Adjacent ovaries are typically fused. However, in *B. richardsonii*, prior to and during anthesis the ovaries are fused only at the base, but as the development continues, the fusion extends to the mid-point (post-genital fusion), producing multiple fruits (Radford et al., 1973). Ovule number varies from 1 to 9; all four nonseptate and three of the septate species (*B. cuspidata*, *B. louvelii*, and *B. taolagnaroensis*) are uniovulate; the remaining 13 septate species are multiovulate.

Placenta size and shape vary between species in *Breonia*. The uniovulate species have small and ovate placentae (Fig. 9F), whereas the multiovulate species have large, flattened, and elongated ones (Fig. 3C, D). The placentae are triangular in *Breonadia*, *Gyrostipula*, and *Janotia* (Fig. 3A, B). Placentae are usually apically attached to the septum, and adnate to the lateral sides of the nectaries, located in the distal center portions of the carpels (see Fig. 13H). These two characters are useful for recognizing *Breonia* from the other Malagasy genera of Naucleaeae, but have never been used for classification by earlier authors. Defining *Breonia* by the placentae attached to the upper third of the septum as originally done by Haviland (1897) in

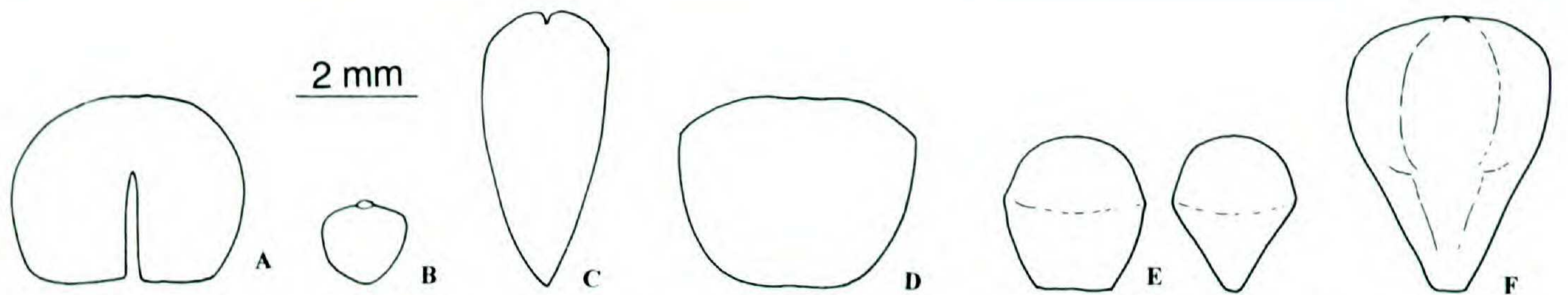


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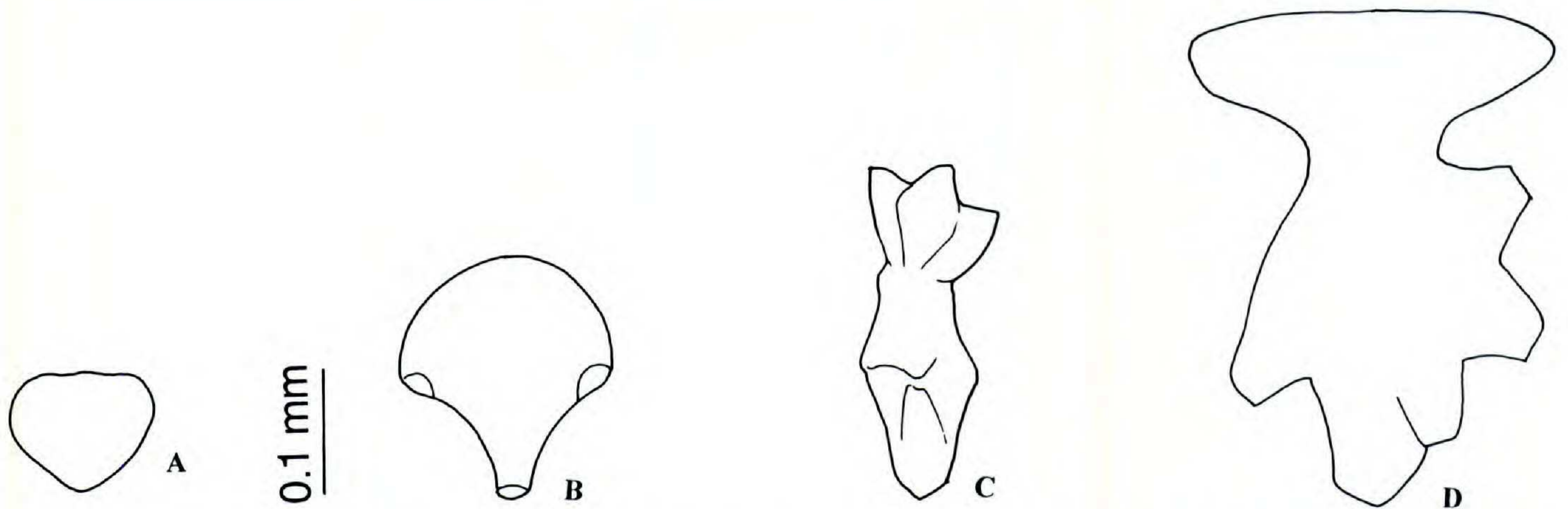


Figure 3. Different shapes of placentae in *Breonia* (C, D) and its allies (A, B). —A. *Gyrostipula foveolata*.—B. *Breonadia salicina*.—C. *Breonia sambiranensis*.—D. *B. macrocarpa*.

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Ovule attachment to the placenta is another useful character that distinguishes *Breonia* from *Breonadia*, *Gyrostipula*, and *Janotia*. In *Breonia*, the ovules are flattened and imbricate (Fig. 4D) along the length of the placentae; they are attached side by side at the base of the placenta in *Breonadia*, *Gyrostipula*, and *Janotia* (Fig. 4A–C).

Breonia stigmas are typically globose to clavate, or rarely capitate, pollen presenters. The receptive areas are always restricted to the top of the stigmatic lobe.

INFRUCTESCENCES

In *Breonia* species the infructescences develop from syncarpous ovaries to form multiple fruits that are fleshy, almost woody, when dry. They are ornamented by accrescent calyces in most species. In *B. fragifera* and *B. decaryana*, the calyx remnants are barely evident and their infructescence surfaces are pusticulate (with small, broad, slight elevations

not high or abundant) and rugose, respectively. In *Breonia*, all the fruits are fused and constitute multiple fruits; the individual fruits are berry-like, bearing 1 to 9 seeds completely enclosed by thin exocarps and thick, hard endocarps.

SEEDS

In *Breonia*, the seeds are usually strongly flattened ellipsoid. Concavo-convex seeds are found in *Breonia chinensis* and *B. stipulata*. *Breonia* seeds are usually unwinged, although rudimentary wings are sometimes observed at both ends (e.g., *B. chinensis* and *B. taolagnaroensis*), or only at the base (e.g., *B. perrieri*). The seeds are possibly released when the corky accrescent disks fall off (see the section on seed dispersal). These disks can be easily removed when the infructescences are still fresh, or after soaking dried ones for several hours. Seed-coat is lineate (e.g., Fig. 6C) in the nonseptate species, and typically reticulate (e.g., Figs. 9C, D, 11C, 14H, 16E) in the septate species.

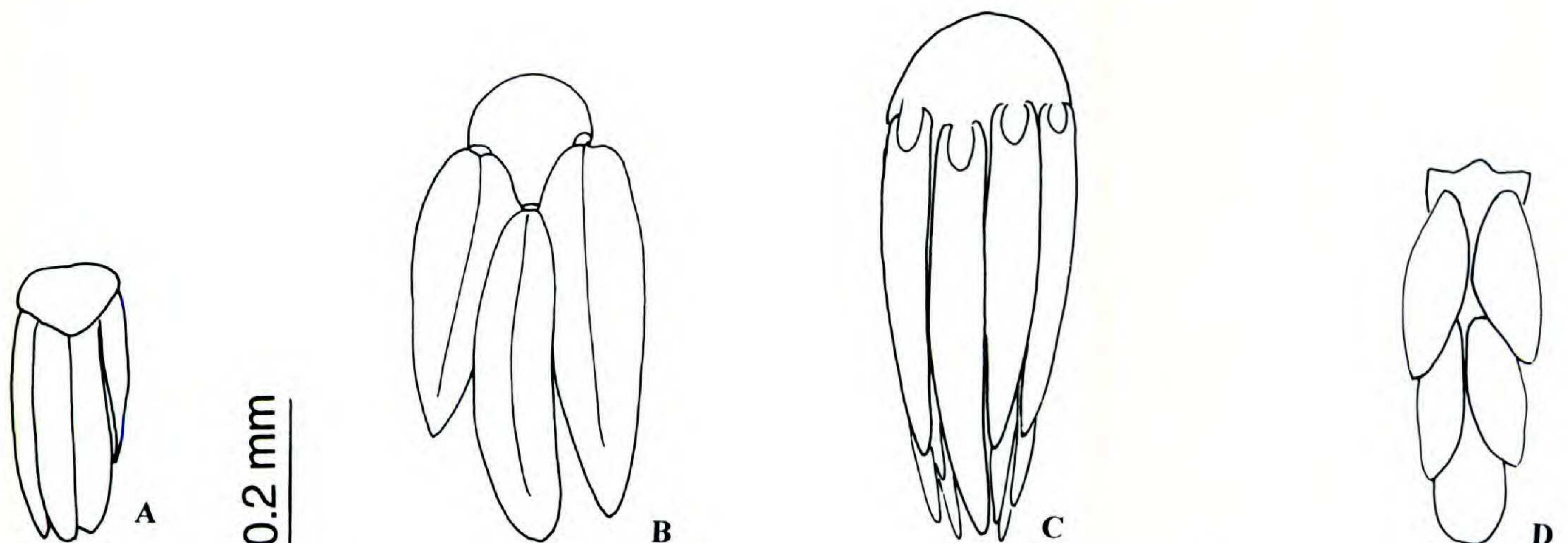


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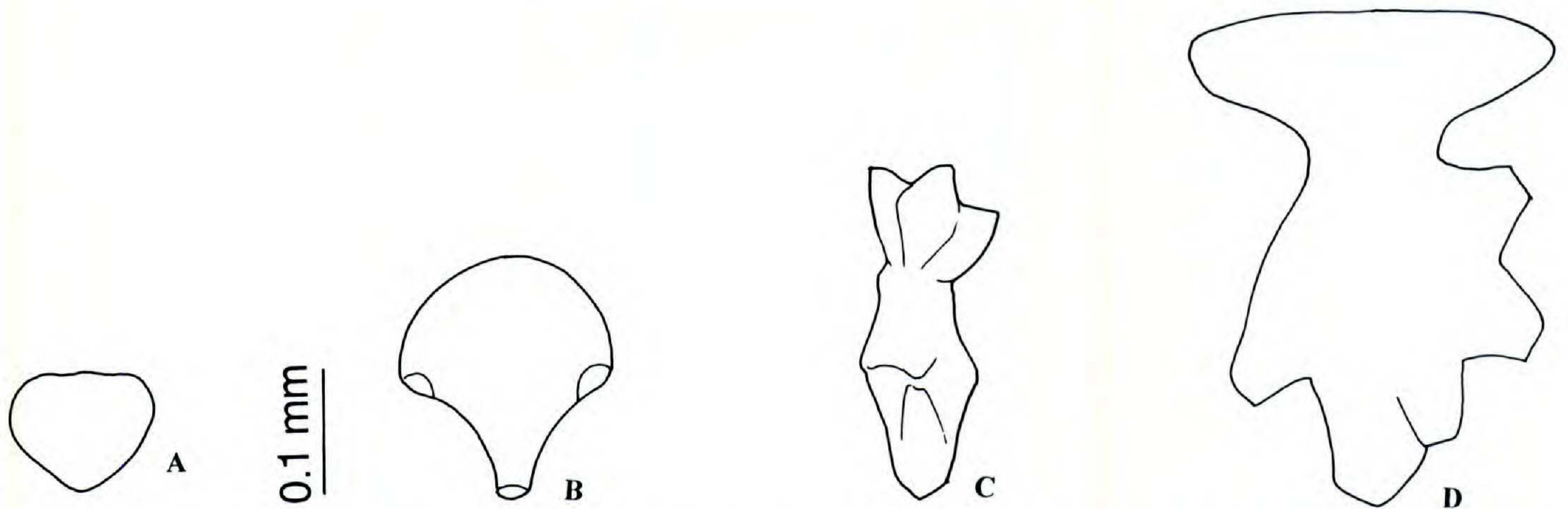


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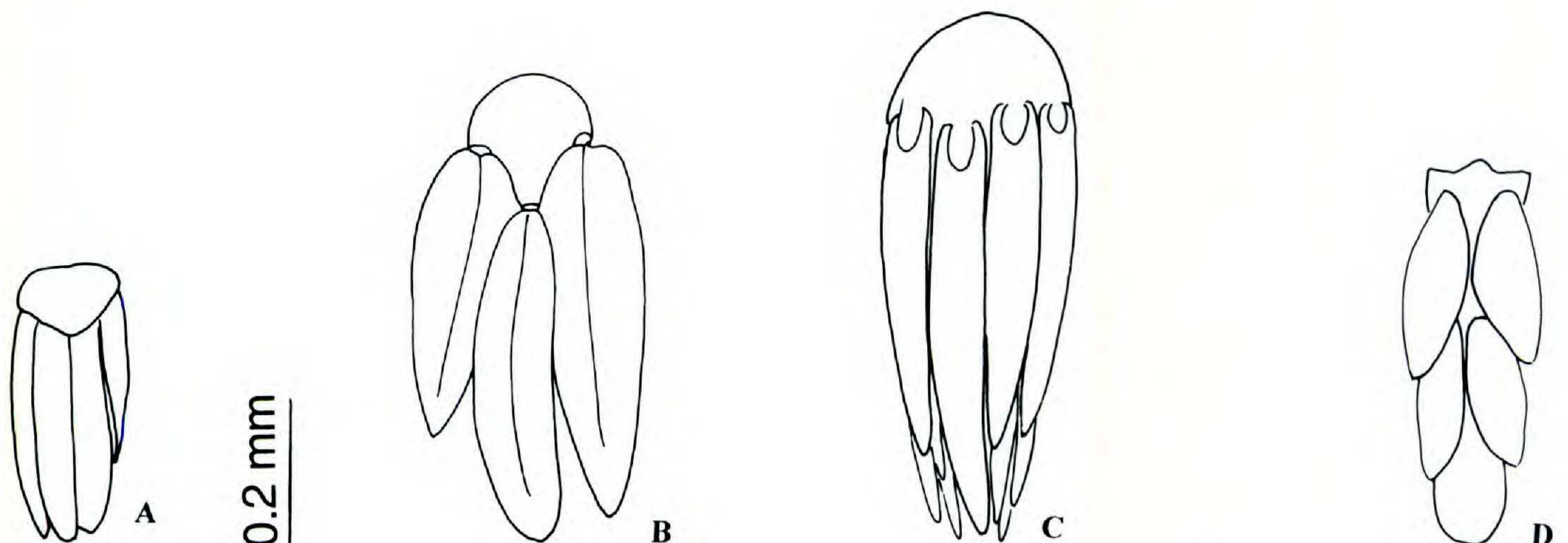


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ECOLOGY

POLLINATION ECOLOGY

How *Breonia* pollinates remains unknown. In the Ankarana Reserve (northern Madagascar) in 1998 I saw the beginning of anthesis in a young individual plant of *B. perrieri*. Flowers in each inflorescence opened simultaneously to emit an intense odor of nectar, which might attract visitors from considerable distance. The plant was visited by several honeybees for a few hours.

DIASPORE DISPERSAL

Entire infructescences. In *Breonia*, the entire infructescence can function as a dispersal unit. In 1998, I observed in the Anjanaharibe Sud Reserve (northeastern Madagascar) a number of mature infructescences of *B. chinensis*, a facultative rheophyte, floating on the river. The corky accrescent disks may act as flotation devices allowing the infructescences to float until they reach the riverbank, where they may be eaten by any frugivores. After flower fall, the nectaries have a new function, as cork-like seed releasers.

A different floating device has also been reported on the seed-coat of the African Naucleaeae *Sarcocephalus pobeguini* Pob. ex. Pell., which is a facultative rheophyte (Abbiw, 1985). Abbiw collected mature seeds of *Nauclea diderrichii* (De Wild. & T. Durand) Merr. and *Sarcocephalus latifolius* (Smith) Bruce (both terrestrial species), as well as *S. pobeguini*. A simple experiment was performed by soaking the seeds of each species in separate containers of water. After 24 hours, the water was poured off: seeds of *Nauclea diderrichii* and *S. latifolius* lay at the bottom of the containers, whereas those of *S. pobeguini* were still floating. *Nauclea diderrichii* and *S. latifolius* seeds were noted to sink after only a few minutes of immersion. The seed-coat apparently acts as a floating device preventing the seeds from sinking.

Seeds. Infructescences of *Breonia* are used as food by all species of Malagasy lemurs. In Lokobe Reserve (Nosy Be District, Antsiranana Province, in northern Madagascar), *B. boivini* and *B. sambiranensis* were the second most important food item in the diet of the black lemur (*Eulemur macaco*) in early 1992. Thirteen percent and 25% of its feeding time during January and February, respectively, were spent on these two species of *Breonia* (Birkinshaw, 1995). Birkinshaw frequently observed intact seeds of *B. boivini* and *B. sambiranensis* in lemur droppings. He found that 2 of 7 defecated seeds germinated, compared with 7 of 30 seeds collected from the ripe infructescences used as a control. The ma-

ture infructescences were not observed to be eaten by any other frugivores in the Lokobe Reserve. Both species of *Breonia* also occur in the Ambanja region where *Eulemur macaco* is also known to be common, suggesting that *E. macaco* may be an effective agent of seed dispersal for *B. boivini* and *B. sambiranensis*. Notably, *B. sambiranensis* is known from only two specimens outside of the Sambirano regions. Seed dispersal mechanisms for other *Breonia* species remain unknown.

ECONOMIC USES

All Malagasy Naucleaeae are known under the local name "Valotra" or "Valotro," meaning that which is reserved for a particular use (Boiteau, 1985). From the 19th century through the mid 20th century, the Malagasy Naucleaeae were used for posts placed around villages to protect against enemies. All *Breonia* have various local uses such as boats, bridges, making handcrafts and furniture, and for general construction purposes because they produce high-quality, hard wood. Several species are used medicinally. The infructescences of *Breonia* are eaten by animals and humans.

SYSTEMATIC POSITION OF *BREONIA* SENSU RAZAFIM.
IN NAUCLEAEAE SENSU RAZAFIM. & BREMER

Breonia has been placed in quite different tribes over the last 170 years. Richard (1830) and De Candolle (1830) placed *Breonia* in the tribe Opercularieae along with other tribes with pluriovular locules. Endlicher (1841) placed the genus in his subtribe Sarcocephalinae (of the tribe Gardenieae), along with *Sarcocephalus*, *Zuccarinia* Blume [= *Jackiopsis* Ridsdale], *Lucinaea* DC. [= *Schradera* Vahl], and *Canephora* Juss. Schumann (1891), followed by Haviland (1897), Verdcourt (1958), Ridsdale (1975), and Robbrecht (1988, 1994), placed *Breonia* in the tribe Naucleaeae based on its compact spherical inflorescences. However, Bremekamp (1966) transferred *Breonia*, along with *Adina* Salisb., *Mitragyna* Korth., *Uncaria* Schreb., and *Neonauclea* Merrill, from the tribe Naucleaeae to the tribe Cinchoneae, arguing that they differ from the other genera of Cinchoneae in the capituliform inflorescence only. All these genera, with the exception of *Breonia*, have capsular fruits with winged seeds, which are characteristic of Cinchoneae. Bremekamp provisionally placed these genera in a separate subtribe within Cinchoneae based on their capituliform inflorescences. Evidence from recent molecular studies based on ITS and *rbcL* sequence data (Razafimandimbison & Bremer, 2002) strongly suggests that *Breonia* belongs to Naucleaeae

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How *Breonia* pollinates remains unknown. In the Ankarana Reserve (northern Madagascar) in 1998 I saw the beginning of anthesis in a young individual plant of *B. perrieri*. Flowers in each inflorescence opened simultaneously to emit an intense odor of nectar, which might attract visitors from considerable distance. The plant was visited by several honeybees for a few hours.

DIASPORE DISPERSAL

Entire infructescences. In *Breonia*, the entire infructescence can function as a dispersal unit. In 1998, I observed in the Anjanaharibe Sud Reserve (northeastern Madagascar) a number of mature infructescences of *B. chinensis*, a facultative rheophyte, floating on the river. The corky accrescent disks may act as flotation devices allowing the infructescences to float until they reach the riverbank, where they may be eaten by any frugivores. After flower fall, the nectaries have a new function, as cork-like seed releasers.

A different floating device has also been reported on the seed-coat of the African Naucleaeae *Sarcocephalus pobeguini* Pob. ex. Pell., which is a facultative rheophyte (Abbiw, 1985). Abbiw collected mature seeds of *Nauclea diderrichii* (De Wild. & T. Durand) Merr. and *Sarcocephalus latifolius* (Smith) Bruce (both terrestrial species), as well as *S. pobeguini*. A simple experiment was performed by soaking the seeds of each species in separate containers of water. After 24 hours, the water was poured off: seeds of *Nauclea diderrichii* and *S. latifolius* lay at the bottom of the containers, whereas those of *S. pobeguini* were still floating. *Nauclea diderrichii* and *S. latifolius* seeds were noted to sink after only a few minutes of immersion. The seed-coat apparently acts as a floating device preventing the seeds from sinking.

Seeds. Infructescences of *Breonia* are used as food by all species of Malagasy lemurs. In Lokobe Reserve (Nosy Be District, Antsiranana Province, in northern Madagascar), *B. boivini* and *B. sambiranensis* were the second most important food item in the diet of the black lemur (*Eulemur macaco*) in early 1992. Thirteen percent and 25% of its feeding time during January and February, respectively, were spent on these two species of *Breonia* (Birkinshaw, 1995). Birkinshaw frequently observed intact seeds of *B. boivini* and *B. sambiranensis* in lemur droppings. He found that 2 of 7 defecated seeds germinated, compared with 7 of 30 seeds collected from the ripe infructescences used as a control. The ma-

ture infructescences were not observed to be eaten by any other frugivores in the Lokobe Reserve. Both species of *Breonia* also occur in the Ambanja region where *Eulemur macaco* is also known to be common, suggesting that *E. macaco* may be an effective agent of seed dispersal for *B. boivini* and *B. sambiranensis*. Notably, *B. sambiranensis* is known from only two specimens outside of the Sambirano regions. Seed dispersal mechanisms for other *Breonia* species remain unknown.

ECONOMIC USES

All Malagasy Naucleaeae are known under the local name "Valotra" or "Valotro," meaning that which is reserved for a particular use (Boiteau, 1985). From the 19th century through the mid 20th century, the Malagasy Naucleaeae were used for posts placed around villages to protect against enemies. All *Breonia* have various local uses such as boats, bridges, making handcrafts and furniture, and for general construction purposes because they produce high-quality, hard wood. Several species are used medicinally. The infructescences of *Breonia* are eaten by animals and humans.

SYSTEMATIC POSITION OF *BREONIA* SENSU RAZAFIM.
IN NAUCLEAEAE SENSU RAZAFIM. & BREMER

Breonia has been placed in quite different tribes over the last 170 years. Richard (1830) and De Candolle (1830) placed *Breonia* in the tribe Opercularieae along with other tribes with pluriovular locules. Endlicher (1841) placed the genus in his subtribe Sarcocephalinae (of the tribe Gardenieae), along with *Sarcocephalus*, *Zuccarinia* Blume [= *Jackiopsis* Ridsdale], *Lucinaea* DC. [= *Schradera* Vahl], and *Canephora* Juss. Schumann (1891), followed by Haviland (1897), Verdcourt (1958), Ridsdale (1975), and Robbrecht (1988, 1994), placed *Breonia* in the tribe Naucleaeae based on its compact spherical inflorescences. However, Bremekamp (1966) transferred *Breonia*, along with *Adina* Salisb., *Mitragyna* Korth., *Uncaria* Schreb., and *Neonauclea* Merrill, from the tribe Naucleaeae to the tribe Cinchoneae, arguing that they differ from the other genera of Cinchoneae in the capituliform inflorescence only. All these genera, with the exception of *Breonia*, have capsular fruits with winged seeds, which are characteristic of Cinchoneae. Bremekamp provisionally placed these genera in a separate subtribe within Cinchoneae based on their capituliform inflorescences. Evidence from recent molecular studies based on ITS and *rbcL* sequence data (Razafimandimbison & Bremer, 2002) strongly suggests that *Breonia* belongs to Naucleaeae

and is closely related to the other Malagasy genera *Breonadia*, *Gyrostipula*, and *Janotia*. It is worth noting that one species of African *Uncaria*, *U. africana* var. *africana*, is also present in Madagascar. These five genera can be identified using the key below.

KEY TO THE GENERA OF MALAGASY NAUCLEAEAE

- 1a. Climbers, paired fang hooks present
..... *Uncaria* Schreb. (1 species)
- 1b. Trees or shrubs, paired fang hooks absent.
- 2a. Hypanthia of the adjacent flowers fused or at least at the base; fruits fused, indehiscent
..... *Breonia* A. Rich. (20 species)
- 2b. Hypanthia of the adjacent flowers free; fruits free, dehiscent.
- 3a. Leaves verticillate; stipules intrapetiolar; interfloral bracteoles present; seeds unwinged
..... *Breonadia* Ridsdale (monotypic)
- 3b. Leaves opposite; stipules interpetiolar; interfloral bracteoles absent; seeds winged.
- 4a. Leaf blades 20–27 × 8–10 cm; stipules of the terminal vegetative buds flattened, complanate; stipules persistent
..... *Janotia* J.-F. Leroy (monotypic)
- 4b. Leaf blades 8–10 × 3–5 cm; stipules of the terminal vegetative buds convolute; stipules deciduous
..... *Gyrostipula* J.-F. Leroy (2 species, 1 of which is yet to be described)

RELATIONSHIPS AMONG SPECIES

Species of *Breonia* can be subdivided into two distinct groups based on the following characters: (1) a group with reduced calyces, coherent carpels, non-septate, and with lineate seed-coat (*Breonia capuronii*, *B. decaryana*, *B. fragifera*, and *B. sphaerantha*); and (2) a group with well-developed calyces, syncarpous carpels, septate, and with reticulate seed-coat (remaining species). The monophyly of these two groups needs to be tested using fast-evolving markers.

The included key to *Breonia* species does not reflect the above relationships; instead, I propose a more practical key that puts more emphasis on the most obvious unique vegetative character states, such as the shape and arrangement of the stipules of the terminal vegetative buds and size of leaf blades.

TAXONOMIC TREATMENT

Breonia A. Rich., in DC., Prodr. 4: 620. Sep. 1830.
TYPE: *Breonia madagascariensis* A. Rich.

Cephalidium A. Rich., Mém. Fam. Rubiacées. 210. Dec. 1830. TYPE: *Cephalidium citrifolium* A. Rich. [= *Breonia chinensis*].

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Elattospermum Sol., Bull. Herb. Boissier 1: 277. 1893.
TYPE: *Elattospermum longipetiolatum* Sol. [= *B. sphaerantha*].

Neobreonia Ridsdale, Blumea 22: 546. 1975. TYPE: *Breonia decaryana* Homolle.

Trees or emergent trees, or rarely shrubs. Bark gray. Stipules of terminal vegetative buds conical or rarely ovate to obovate, obvolute or rarely complanate, glabrous or pubescent. Leaves simple, opposite, decussate, persistent or deciduous; domatia present in axils of secondary veins or rarely tertiary veins or absent; stipules interpetiolar, mostly cymbiform or rarely complanate, deciduous or rarely semi-persistent, entire. Inflorescences usually solitary or sometimes 2 or rarely 4 to 8 per axil, axillary, globose; inflorescence axes unbranched or rarely branched, flattened or terete, usually slender or rarely robust and woody, glabrous to pubescent, articulated or not; bracts usually calyptra-like, cohering and completely enclosing the young inflorescence, separating longitudinally into two equal hemispherical shells, remaining attached to the node for a few days and then falling off; peduncles elongated (as internode above the inflorescence axis) or not. Flowers hermaphroditic, radially symmetrical, mostly 5-merous or sometimes 4-merous, closely congested, sessile; calyx tubes infundibular, inside usually densely pubescent, outside glabrous except for a few straight long hairs around the base, free from others or rarely fused; calyx lobes oblong to truncate, densely pubescent; corolla tubes hypocrateriform, inside glabrous to puberulous, outside glabrous; corolla lobes oblong, glabrous or puberulous to pubescent, aestivation imbricate in bud; stamens 5 or rarely 4, inserted on the throat of the corolla tubes; anthers introrse, partly exerted, dehiscing by longitudinal slits, basifixed; filaments short, flattened, glabrous; stigmas 1 per flower, clavate to globose or slightly cylindrical, exerted from the corolla tubes, pollen presenters; receptive areas restricted to the top of the stigmatic lobe; ovary of an individual flower always bicarpellate, syncarpous or coherent, adjacent ovaries typically syncarpous or rarely fused at the base; ovules 1 to 9 per locule, strongly flattened, pendulous, imbricate; placentae apically attached to the septum, usually elongated, flattened, adnate to the septum; floral nectary epigynous, embedded in the hypanthium between the base of the corolla tube and the apex of the ovary. Infructescences formed by multiple fruits, globose, with persistent calyx remnants. Individual fruits berry-like; endocarps hard and glossy or sometimes fibrous and soft; disks accrescent, conspicuous, variable in size; seeds usually strongly flattened, sometimes concavo-convex, or plano-convex, ellipsoid, not alate or rarely with rudimentary wings, red; seed-coat reticulate or lineate.

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KEY TO *BREONIA* SPECIES

- 1a. Stipules of terminal vegetative buds flattened, complanate; inflorescences 4 to 8 per axil 5. *B. decaryana*
- 1b. Stipules of terminal vegetative buds conical, obvolute; inflorescences usually 1 or rarely 2 per axil.
- 2a. Lower surfaces of leaf blades always pubescent, tuft-domatia present in the axils of secondary and tertiary veins 10. *B. macrocarpa*
- 2b. Lower surfaces of leaf blades always glabrous, tuft-domatia absent in the axils of secondary and tertiary veins.
- 3a. Leaf blades 45 × 25 cm; inflorescence axes 16–21 cm long 11. *B. madagascariensis*
- 3b. Leaf blades less than 32 × 16 cm; inflorescence axes less than 13 cm long.
- 4a. Stipules semi-persistent 19. *B. tayloriana*
- 4b. Stipules deciduous.
- 5a. Leaf blades with the 3 secondary veins diverging from the base of the midrib, base cordate 13. *B. perrieri*
- 5b. Leaf blades without 3 secondary veins diverging from the base of the midrib, base noncordate.
- 6a. Bracts tubular, terminated by 3 or 4 broadly triangular lobes, never surrounding the young inflorescence, persistent; adjacent ovaries fused at the base only 14. *B. richardsonii*
- 6b. Bracts calyptra-like, surrounding the young inflorescence, deciduous; adjacent ovaries completely fused.
- 7a. Adjacent calyx tubes completely fused; infructescences with barely evident calyx remnants 6. *B. fragifera*
- 7b. Adjacent calyx tubes free; infructescences with well-developed calyx remnants.
- 8a. Corolla lobes pubescent to puberulous, recurved.
- 9a. Leaf blades with glabrous cryptic-type domatia on lower surface, swollen on upper surface; fertile peduncles densely pubescent; calyx tubes uniquely dilated above the middle and constricted at both ends 20. *B. tsaratananensis*
- 9b. Leaf blades without domatia; fertile peduncles glabrous; calyx tubes funnel-shaped.
- 10a. Lower surfaces of leaf blades yellow-red-tinged when dry; calyx tubes 1–1.2 mm long; lobes 0.2–0.3 mm long, bearing shallow depressions on the center and a short protuberance on the edge toward the style 15. *B. sambiranensis*
- 10b. Lower surfaces brown-tinged when dry; calyx tubes 2.5–3 mm long; lobes 2–2.2 mm long, without shallow depressions, without protuberance 1. *B. boivinii*
- 8b. Corolla lobes glabrous and not recurved.
- 11a. Inflorescence axes terete; ovaries coherent but not histologically fused, nonseptate.
- 12a. Petioles 1.5–2 cm long; secondary veins drying red-tinged 16. *B. sphaerantha*
- 12b. Petioles always more than 2 cm long; secondary veins drying yellow-tinged 2. *B. capuronii*
- 11b. Inflorescence axes flattened; ovaries fused, septate.
- 13a. Stipules of terminal vegetative buds 15–22 mm long.
- 14a. Leaf blades obovate, always wavy when dry 7. *B. havilandiana*
- 14b. Leaf blades elliptic to lanceolate, not wavy when dry 17. *B. stipulata*
- 13b. Stipules of terminal vegetative buds 4–10 mm long.
- 15a. Ovaries uniovulate.
- 16a. Leaf blades 9–16 × 3.5–6.5 cm long, ovate to oblong in shape 18. *B. taolagnaroensis*
- 16b. Leaf blades 4–9 × 1.5–3.5 cm long, oblanceolate in shape.
- 17a. Leaf blade apices acute, base cuneate; fertile peduncles 2–4 cm long 8. *B. louvelii*
- 17b. Leaf blade apices caudate, bases attenuate; fertile peduncles 4.5–6.5 cm long 4. *B. cuspidata*
- 15b. Ovaries multiovulate (2 to 9 ovules per locule).
- 18a. Petioles 3–6 mm long 12. *B. membranacea*
- 18b. Petioles at least 9 mm long.

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- 19a. Stipules of terminal vegetative buds more than 5–6 mm long; inside of calyx tubes pubescent; 2–4 ovules per locule 3. *B. chinensis*
- 19b. Stipules of terminal vegetative buds 3 mm long; inside of calyx tubes glabrous; more numerous ovules (7–9) per locule 9. *B. lowryi*

1. *Breonia boivinii* Havil., J. Linn. Soc. Bot. 33: 35. 1897. TYPE: Madagascar. [Antsiranana province], District Nosy be [without exact locality], *Boivin s.n.* (holotype, K!; isotype, P not seen).

Shrubs, ca. 7 m tall. Bark rugose. Leafy stems terete, glabrous. Stipules of terminal vegetative buds conical, 5–7 × ca. 5 mm, glabrous. Leaves persistent; petioles (10–)15–25 × ca. 4 mm, terete, glabrous; blades 11.5–23 × 4.5–13.5 cm, ovate to broadly obovate, glabrous, coriaceous, glossy, apex acute to rounded, base cuneate, lower surfaces brown-tinged when dry; margins glabrous, entire; secondary veins ca. 9 pairs per side, eucamptodromous; tuft-type domatia in the axils of midribs or absent; stipules 6–9 × ca. 6 mm, cymbiform,

sometimes emarginate, not carinate, glabrous, free at the base, deciduous. Inflorescences solitary; heads 3.5–3.8 cm wide, including stigmas; inflorescence axes 2–4(–6.7) cm long, quadrangular to slightly flattened, glabrous; bracts calyptra-like, deciduous; peduncles (2.5–5)15–25 mm long. Flowers 5-merous; calyx tubes 2.5–3 mm long, prominently ribbed, glabrous, dilated above the middle, constricted at both ends, lobes 2–2.2 mm long, truncate, prominently ribbed, inside puberulous to tomentose, outside glabrous, toward the base of lobes tomentose; corolla tubes 6–7 × ca. 0.5 mm, glabrous; lobes 3–3.1 mm long, oblong, recurved, ciliate, inside puberulous with a few scattered long hairs around the apex, outside glabrous; anthers ca. 1.5 mm long; filaments ca. 0.5 mm long, glabrous,

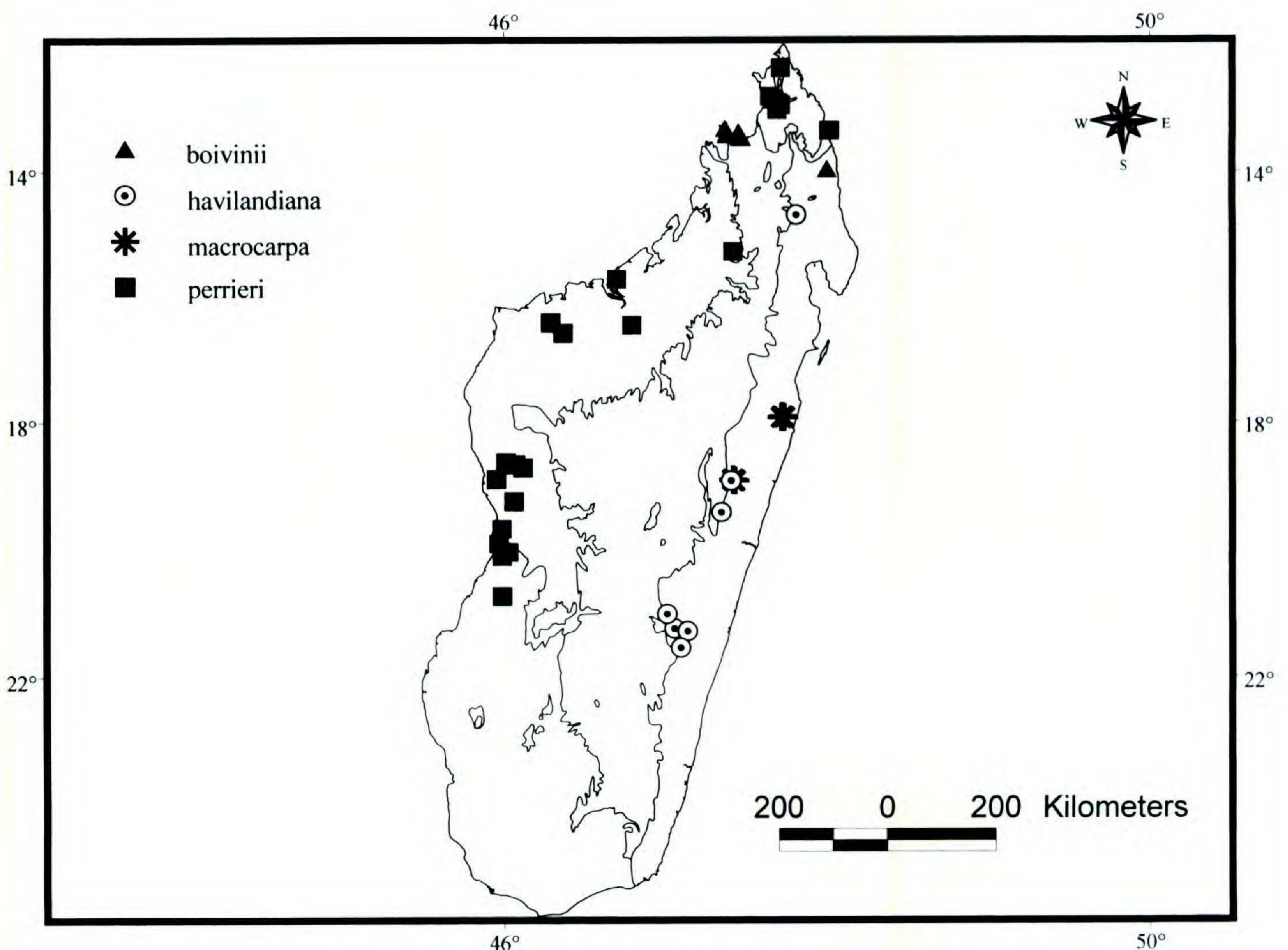


Figure 5. Distribution of *Breonia boivinii*, *B. havilandiana*, *B. macrocarpa*, and *B. perrieri*.

- 19a. Stipules of terminal vegetative buds more than 5–6 mm long; inside of calyx tubes pubescent; 2–4 ovules per locule 3. *B. chinensis*
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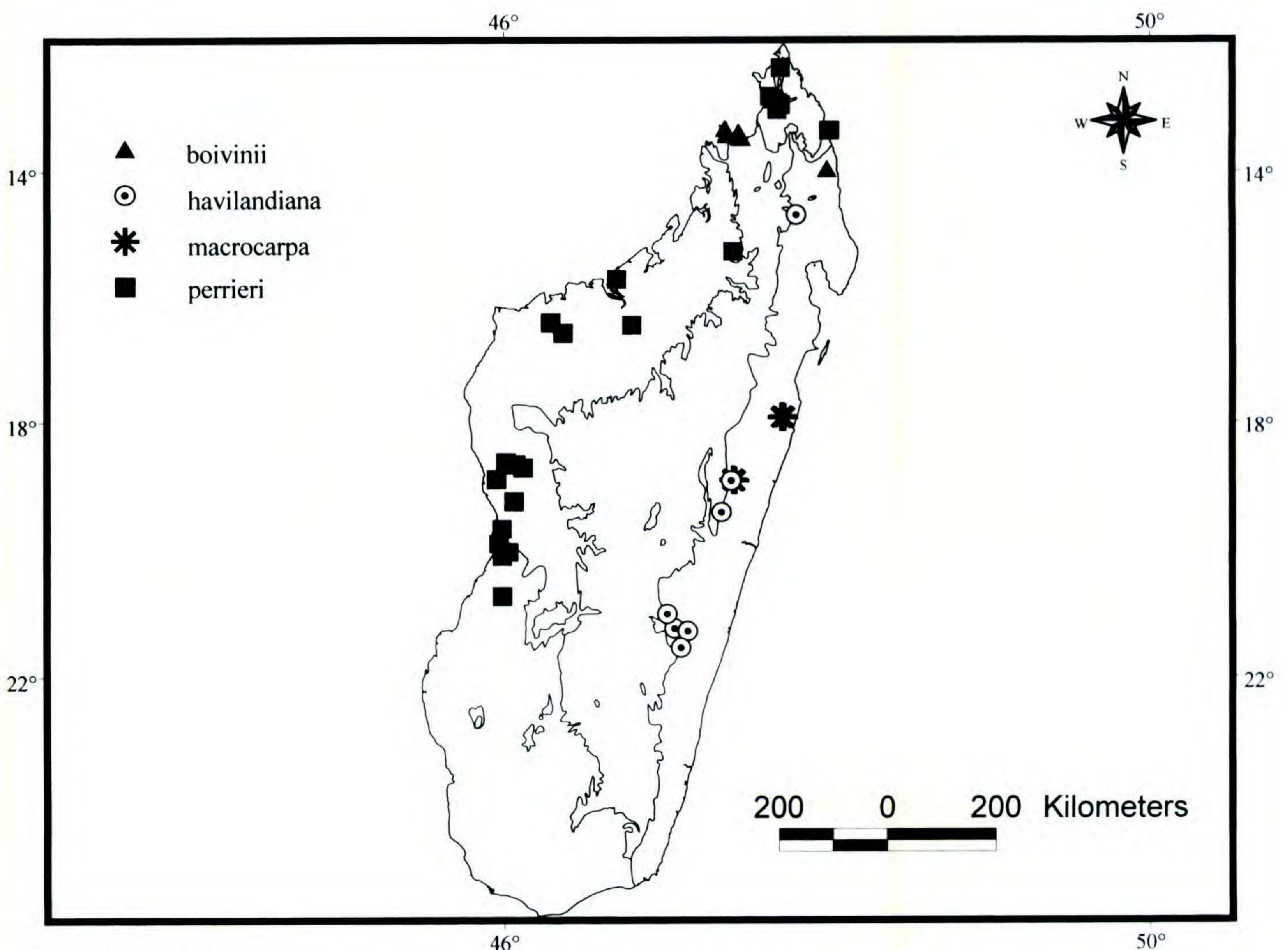


Figure 5. Distribution of *Breonia boivinii*, *B. havilandiana*, *B. macrocarpa*, and *B. perrieri*.

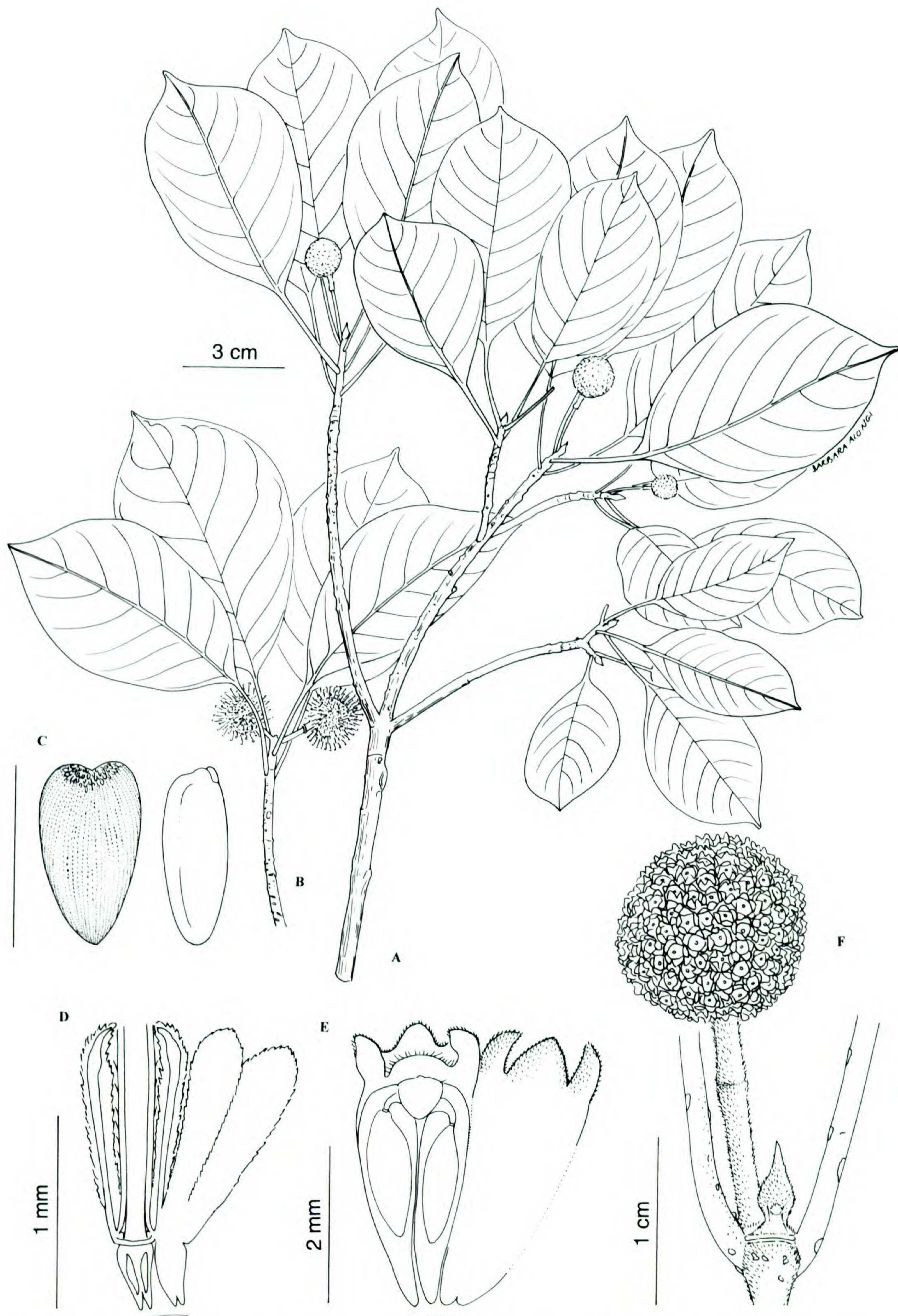


Figure 6. *Breonia capuronii*.—A. Fertile branch with infructescences. —B. Fertile branch with inflorescences. —C. Seed: dorsal view (left); lateral view (right). —D. Two adjacent flowers, showing two adjacent ovaries separated: dissection through corolla and calyx tubes and an ovary of one flower (left); separate flower (right). —E. Median

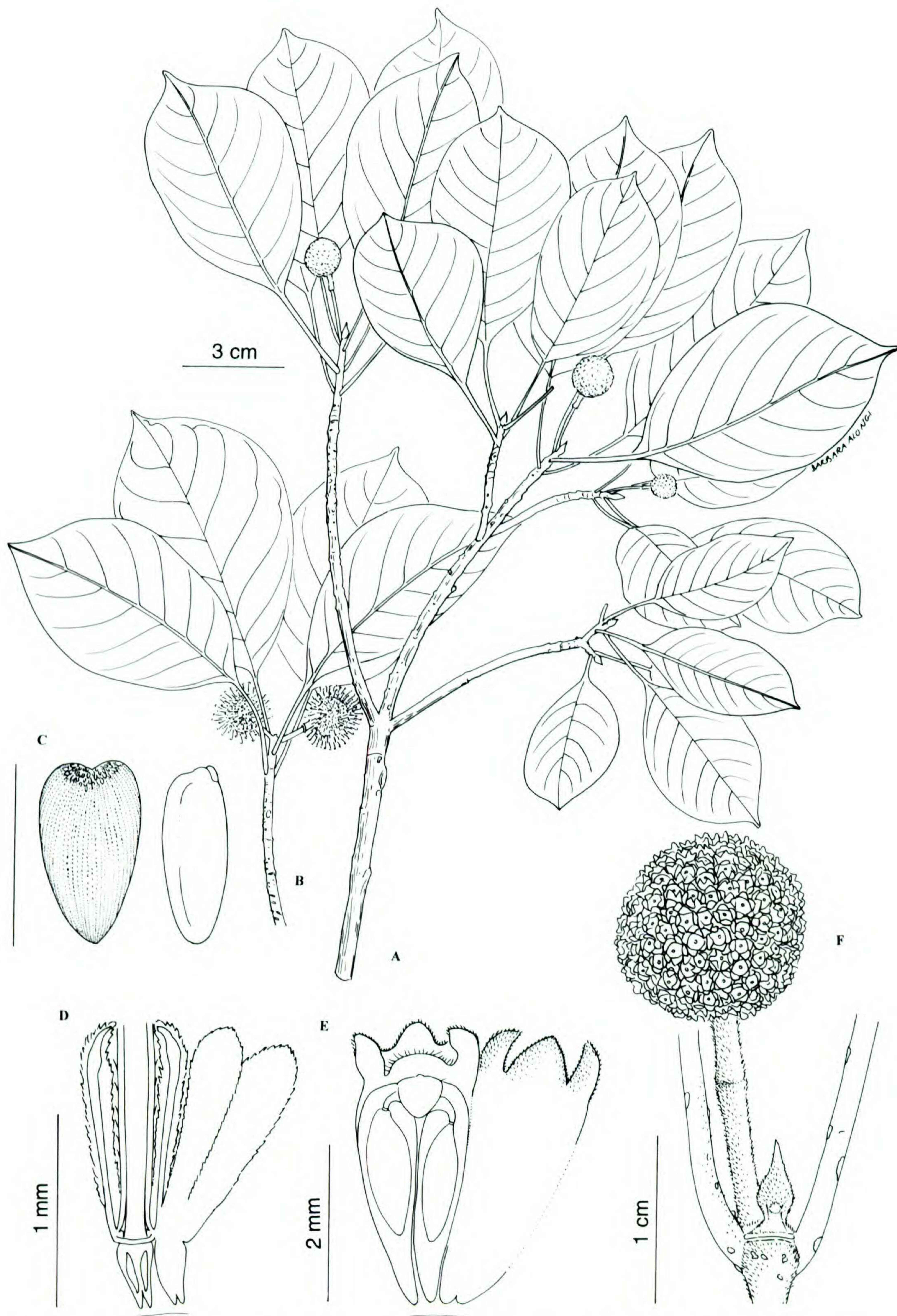


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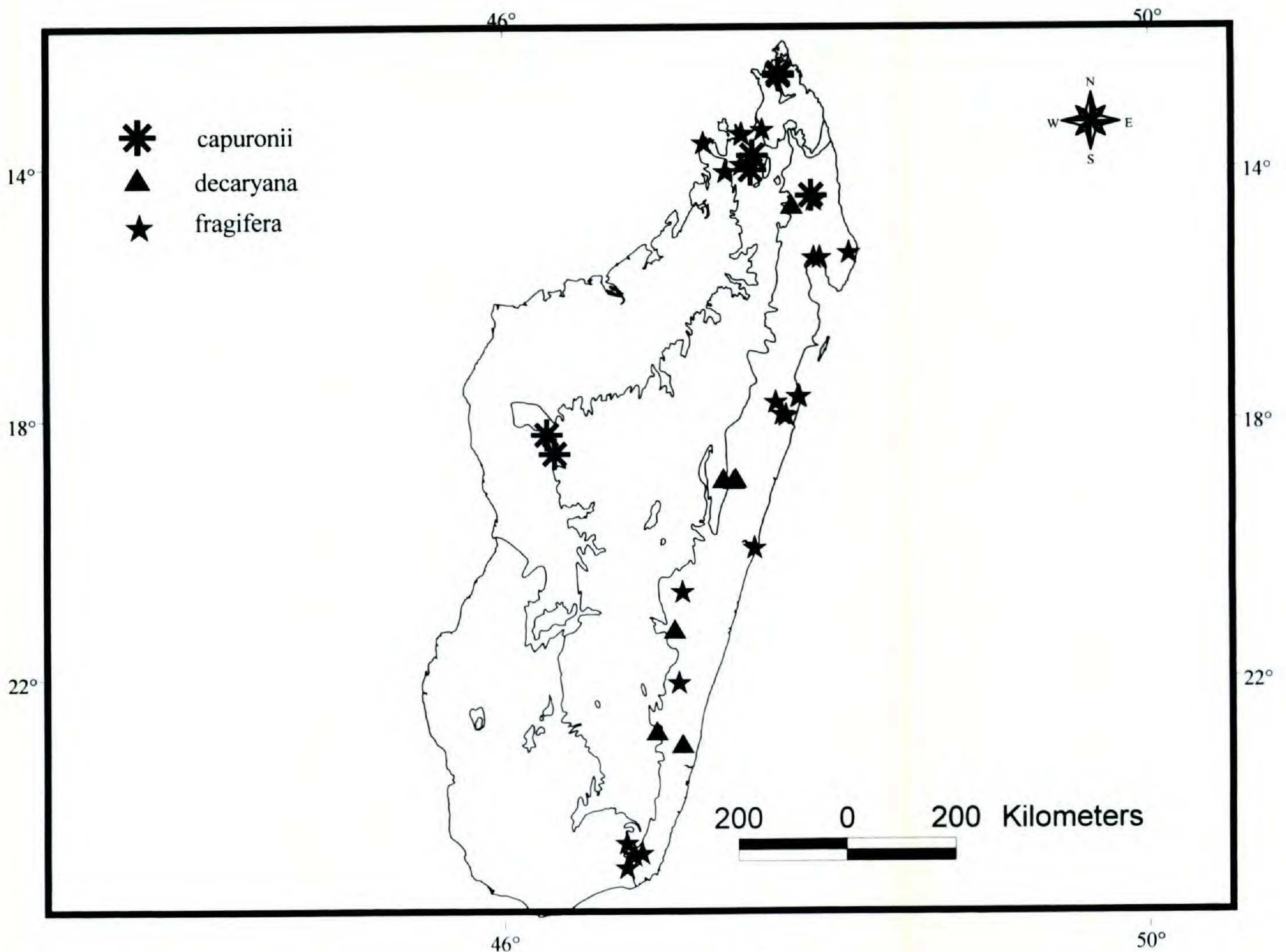


Figure 7. Distribution of *Breonia capuronii*, *B. decaryana*, and *B. fragifera*.

flattened; styles 8–9 mm long, stigmas capitate; ovary 2-carpellate; carpels syncarpous; ovules 6 per locule, pendulous, imbricate; placentae flattened. Infructescences 3–3.5 cm diam., with well-developed calyx remnants; fruits with endocarp soft and fibrous; disks accrescent, obconical; seeds 4 to 6 per locule, strongly flattened, ellipsoid, white-tinged; seed-coat reticulate.

Habitat and distribution. Low- and mid-altitude evergreen rainforests; Districts of Nosy be, Ambanja (Sambirano regions) and Vohémar (Fig. 5).

Common name. Valotro (which is reserved for a particular use).

Phenology. Flowering November to December; fruiting January to February.

Additional specimens examined. MADAGASCAR. **Antsiranana:** District Nosy be, Réserve Intégrale de Lokobe, *Antilahimena* 19 (MO), *Antilahimena* 44 (MO), 2751 RN (P), *Birkinshaw* 67 (K, MO, P, TAN); Ankify,

1432 SF (TEF); Doanilahy, 4905 RN (TAN), 6234 RN (TEF); District Ambanja, Presqu'Île d'Ambato, 23424 SF (TEF), *Randrianaivo* 247 (MO), *Ursch* s.n. (P); District Vohémar, Canton Antsirabe-Nord, Forêt d'Analamateza, 27593 SF (TEF), 27636 SF (TEF).

2. *Breonia capuronii* Razafim., sp. nov. TYPE: Madagascar. [Antsiranana province], Massif de Montagne d'Ambre, around "Station forestière des Roussettes," ca. 800–1000 m, 15 Feb. 1962 (fl, young infr.), 22059 SF (holotype, TEF). Figures 1C and 6.

Haec species ad congeneros nonnullos loculis uniovulatis accedit, sed ab eis petiolo longo (semper 2 cm excedente) atque foliorum nervis secundariis in sicco flavidis distinguitur.

Trees, 15–30 m tall. Bark white-tinged, rugose. Leafy stems terete, puberulous to pubescent, lenticellate. Stipules of terminal vegetative buds conical, 4–5 × 1.5–2 mm, puberulous. Leaves decid-

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dissection of developed post-anthesal mature flower showing calyx remnant, accrescent disk, and the single seed per locule (left); entire fruit (right). —F. Portion of branch apex with a mature infructescence, a stipule of terminal vegetative bud, and two petioles. A–D from 22059 SF (TEF) and E, F from 18518 SF (TEF).

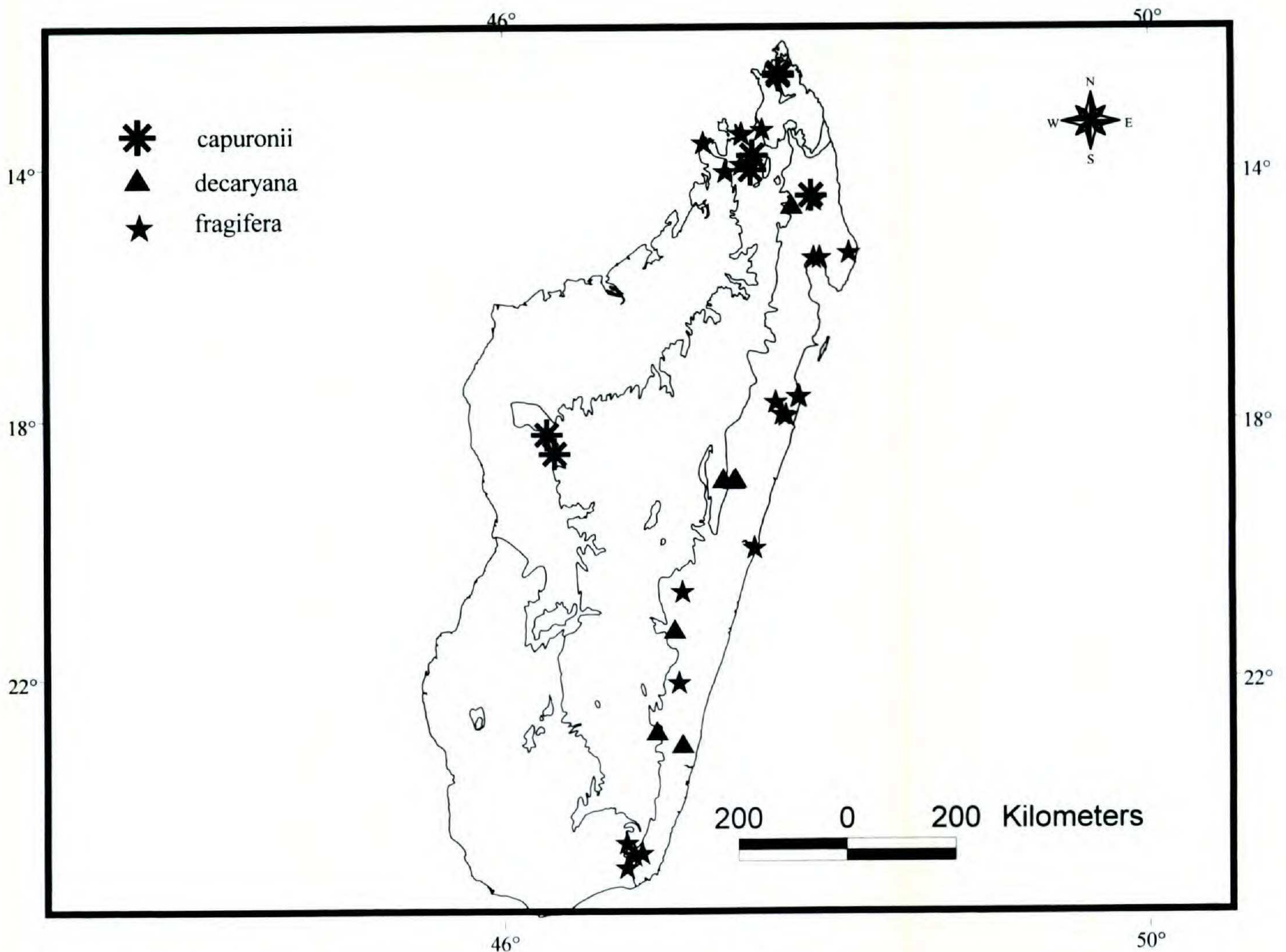


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Common name. Valotro (which is reserved for a particular use).

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1432 SF (TEF); Doanilahy, 4905 RN (TAN), 6234 RN (TEF); District Ambanja, Presqu'île d'Ambato, 23424 SF (TEF), *Randrianaivo* 247 (MO), *Ursch s.n.* (P); District Vohémar, Canton Antsirabe-Nord, Forêt d'Analamateza, 27593 SF (TEF), 27636 SF (TEF).

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uous; petioles 22–35 × ca. 1 mm, terete, glabrous, lenticellate; blades 9.2–11.5 × 5.3–7.8 cm, broadly elliptic to obovate, clustered near the stem apices, glabrous, membranaceous, glossy, apex acute to mucronate, base rounded; margins glabrous, entire; secondary veins ca. 8 pairs per side, eucamptodromous, adaxially conspicuous, yellow-tinged; domatia absent; stipules ca. 4 mm long, cymbiform, not carinate, glabrous, free at the base, deciduous. Inflorescence solitary; heads ca. 2 cm wide; inflorescence axes ca. 1.7 cm long, twisted when dry, terete, densely puberulous; bracts calyptra-like, deciduous; peduncles ca. 1 mm long, densely pubescent. Flowers typically 4-merous; calyx tubes ca. 1 mm long, green-yellow-tinged, inside velutinous, outside pubescent, lobes 0.7–0.9 mm long, triangular, pubescent; corolla tubes 2.8–3.0 × 0.2–0.5 mm, glabrous; lobes ca. 1.5 mm long, oblong, glabrous, toward the apex gradually puberulous, ciliate; anthers ca. 0.5–1 mm long; filaments ca. 0.2 mm long, glabrous, terete; styles 7.8–8 × ca. 0.1 mm, glabrous; stigmas globose or clavate; ovary 2-carpellate; carpels coherent; ovule 1 per locule, pendulous; placentae small, elongated. Infructescences 6–10 mm diam., with persistent calyx remnants; individual fruits with endocarp hard, glossy; disks accrescent, obconical; seed 1 per locule, strongly flattened, ellipsoid, red; seed-coat lineate.

Habitat and distribution. Mid-altitude evergreen rainforests and semi-deciduous forests; Districts of Antsiranana II, Ambanja, Sambava, and Tsiroanimandidy (Fig. 7).

Common names. Valodrano (Valotra growing in water), Valotro.

Phenology. Flowering January–February; fruiting March–April.

Discussion. This species is different from the other species of *Breonia* with a single ovule per locule by having long petioles (always more than 2 cm), and secondary leaf veins drying yellow-tinged. It has a large geographical distribution, but appears to be locally rare or perhaps under-collected due to its large size. The type species was collected within the Montagne d'Ambre National Park boundaries.

The specific epithet honors René Capuron, a French botanist based in Madagascar for several years in the mid 20th century who worked mainly on Malagasy woody plant families (including Rubiaceae).

Paratypes. MADAGASCAR. **Antananarivo:** District Tsiroanimandidy, Forêt d'Ambohijanahary, 18518 SF (P, TEF). **Antsiranana:** Montagne d'Ambre National Park, Malcomber et al. 1219 (MO); District Ambanja, Canton Ma-

rovato, Analamateza, 7906 RN (TEF), 12975 RN (TEF); Manongarivo, Gautier 3772 (G, MO, TAN); District Sambava, Canton Maroambihy, Andranomadiohely, 9002 RN (TEF).

3. *Breonia chinensis* (Lam.) Capuron, *Adansonia*, sér. 2, 13: 473. 1973. *Cephalanthus chinensis* Lam., *Encycl. Méth.* 1: 678. 1785. TYPE: "Isle de France" (Mauritius). [Without exact locality], *Commerson s.n.* (holotype, P-LA photo!). Figures 1D and 2E.

Nauclea citrifolia Poir., in Lam., *Encycl. Méth.* 4: 435. 1789. *Cephalidium citrifolium* (Poir.) A. Rich., *Mém. Fam. Rub.* 210. Dec. 1830. *Breonia citrifolia* (Poir.) Ridsdale, *Blumea* 22: 545. 1975. TYPE: Madagascar. [Without exact locality], *collector unknown s.n.* (holotype, P-LA photo!).

Sarcocephalus richardianus Baill., *Adansonia* 12: 312. 1879. *Breonia richardiana* (Baill.) Havil., *J. Linn. Soc. Bot.* 33: 36. 1897. TYPE: Madagascar. [Without exact locality], *Chapelier s.n.* (holotype, P!).

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Sarcocephalus richardii Drake, in A. Grandidier, *Hist. Pl. Madagascar* 36: 457. 1897. *Cephalina richardii* Palacky, *Cat. Pl. Madagascar* 4: 50. 1906. TYPE: *Grandidier t. 457* (not seen).

Shrubs or trees, 7–25 m tall. Bark rugose. Leafy stems quadrangular, glabrous. Stipules of terminal vegetative buds conical, 5–6 × 1–1.3 mm, glabrous. Leaves persistent; petioles 9–15 × ca. 1 mm, adaxially canaliculate, glabrous; blades 6.4–11 × 2.4–5.5 cm, obovate, glabrous, coriaceous, not glossy, apex broadly to narrowly cuspidate, base cuneate; margins glabrous, entire; secondary veins 8 to 11 pairs per side, eucamptodromous, slightly prominulous; domatia absent; stipules 7–11 × 1.5–2.5 mm, cymbiform, carinate, glabrous, free at the base, deciduous. Inflorescence solitary; heads 1–2.5 cm wide; inflorescence axes 3.4–6.5 cm long, glabrous; bracts calyptra-like, deciduous; peduncles 1–2 mm long. Flowers 5-merous; calyx tubes ca. 1.5 mm long, inside lanate, outside glabrous, pubescent toward the base of the lobes, lobes ca. 0.5 mm long, truncate, lanate; corolla tubes 2.5–5 × 0.5 mm, glabrous; lobes 1.5–2 mm long, oblong, glabrous; anthers 1–1.5 mm long; filaments ca. 0.1 mm long, glabrous, flattened; styles 7.5–9 × 0.3–0.4 mm, glabrous; stigmas clavate to capitate; ovary 2-carpellate; carpels syncarpous; ovules 2 to 3 per locule, pendulous, imbricate; placentae elongated. Infructescences 0.7–2 cm diam., with well-developed persistent calyx remnants; individual fruits with endocarp hard, glossy; disks accrescent, ob-

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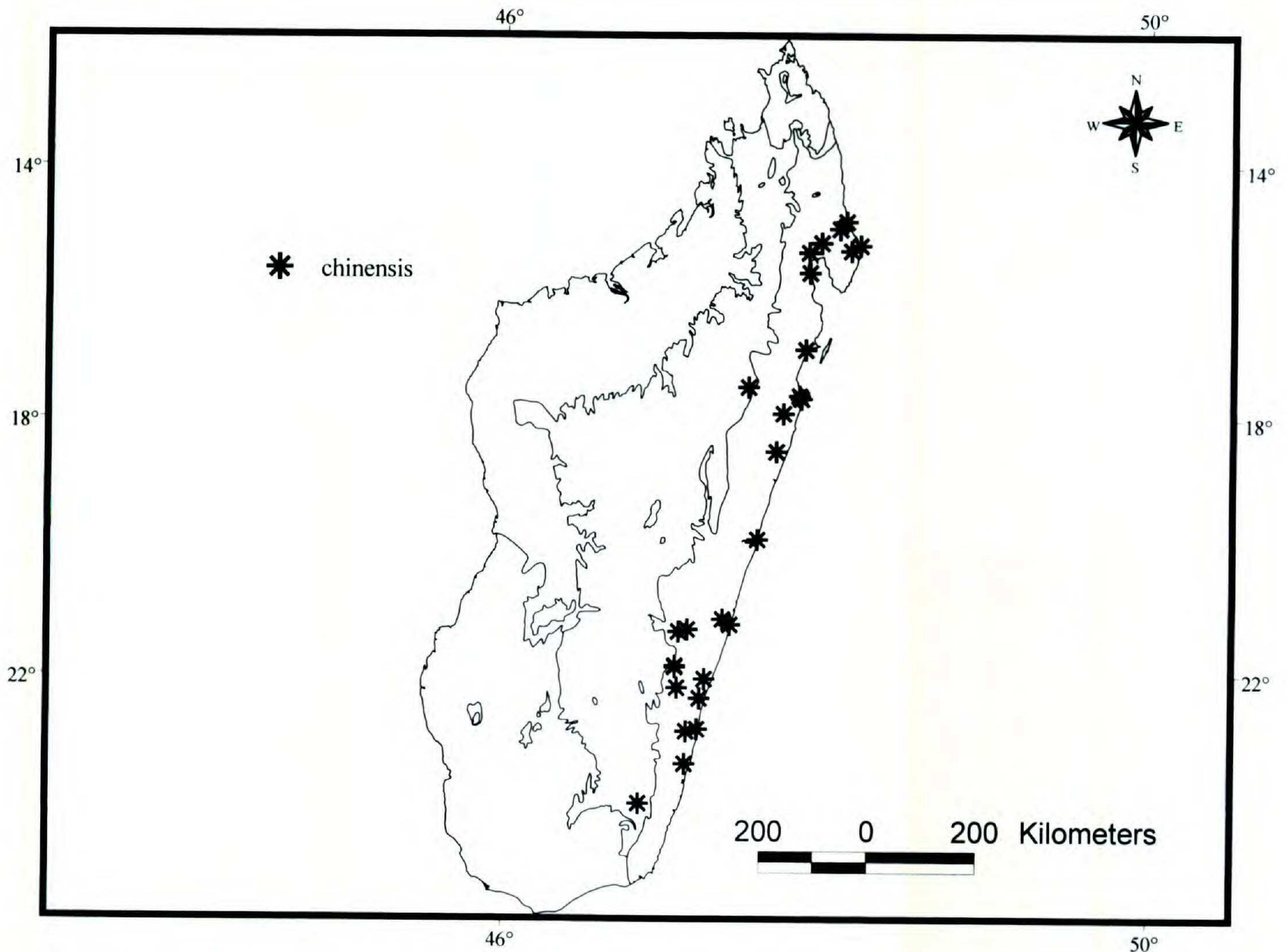


Figure 8. Distribution of *Breonia chinensis*.

conical; seeds 2 to 3 per locule, with rudimentary wings at both ends, strongly flattened, concavo-convex, ellipsoid, red; seed-coat reticulate.

Habitat and distribution. Evergreen rainforests and mid-altitude humid forests, occasionally in dry-land sites and riverbeds; Districts of Antalaha, Sambava, Farafangana, Fort-Carnot, Ifanadiana, Manakara, Mananjary, Vangaindrano, Vohipeno, Brickaville, Mahanoro, Maroantsetra, Soanierana Ivongo, and Vavatenina (Fig. 8).

Common names. Molompangady (lips of Valotra), Valopangady (spade of Valotra), Valotra, Valopotsy (white Valotra), Vavalotra, Voakiringy, and Voamalopangady.

Phenology. Flowering August to October; fruiting November to March.

Discussion. *Breonia chinensis* is the most common species of *Breonia* in Madagascar but grows only in evergreen rainforests. The epithet “*chinensis*” is not the most appropriate choice for *Breonia*, which is restricted to Madagascar; however, it has priority over the other available basionyms. Candidate basionyms of *B. chinensis* were all considered separate species of *Breonia* until Capuron (1973a), endorsed by Bosser (1984, 1999), clarified

the identity of *Cephalanthus chinensis* Lam. as a separate species of *Breonia*. Homolle (1938) reduced *Breonia coriacea* Havil. to synonymy under *B. richardiana* Havil. *Breonia coriacea* was not mentioned by Ridsdale (1975), but both species definitely belong to *Breonia chinensis* based on their leaf blade shape and size, inflorescence axis shape, and ovule number.

It has been accepted that the original description of *Nauclea citrifolia* Poir. [= *B. chinensis*] is in Lamarck’s *Encyclopédie* (1789: 435) and that this species belongs to *Breonia* (Bakhuizen van den Brink, 1970; Ridsdale, 1975; Bosser, 1984, 1999). However, Poiret did not specify type specimens of any of his species. This has caused some confusion as to which specimen he based *N. citrifolia* on and led to disagreement over the identity of the name. Richard (1830: 219) stated that his *Cephalidium citrifolium* (Poir.) A. Rich. was a new combination based on *N. citrifolia* Poir.: “*Nauclea* sp. Poir., *Encycl. méth.*, . . . Species unica observata: *Cephalidium citrifolium*, Nob. (*Nauclea citrifolia*, Poiret, l. c.)” Like Poiret, Richard also did not cite the type specimens of any of his species.

There is one specimen (lacking the collector’s

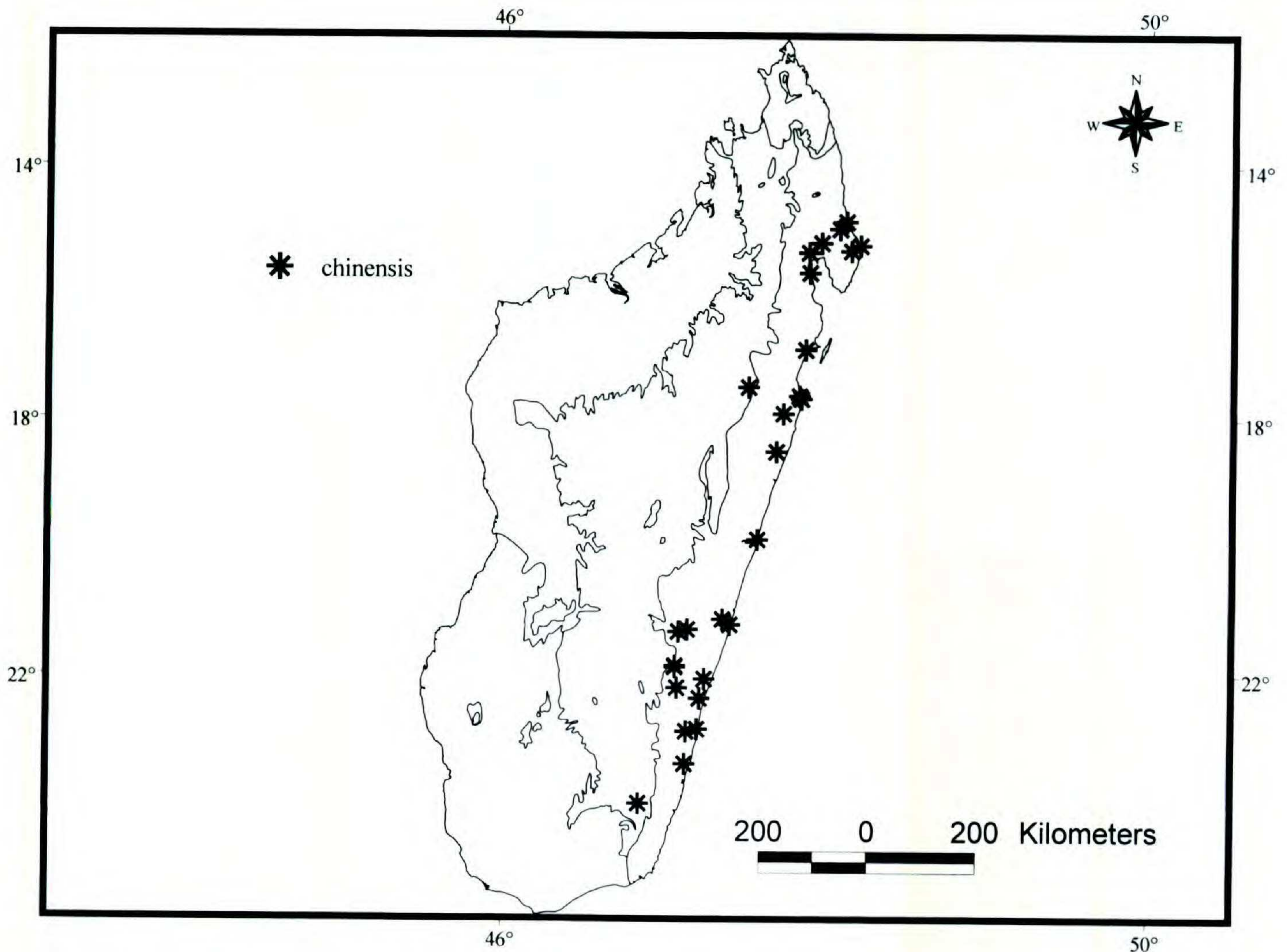


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There is one specimen (lacking the collector’s

name and number) with four labels in P-LA that may be the type of *N. citrifolia* Poir. The first label is Lamarck's and says: "*Nauclea citrifolia* dic n° 2." The second is Roeper's and states: "? 8. *Nauclea cadamba* Roxb.? [and] *Nauclea citrifolia* Poir.!!!, per quem affinis orientalis! immonimis affinis." The third states that this specimen returned to P-LA: Herbar de Lamarck, "acquis en Novembre 1886." The fourth label is that of Capuron and states: "*Breonia chinensis* (Lamk.) R. Capuron." Capuron (1973a) considered that this Lamarck specimen is the type of *Nauclea citrifolia* Poir. and is conspecific with *Breonia chinensis* (Lam.) Capuron. I concur with him because the protologue of *N. citrifolia* Poir. in Lamarck (1789: 435) agrees with this specimen. Ridsdale (1975) also endorsed Capuron's view, but made the new combination *Breonia citrifolia* (Poir.) Ridsdale because he did not recognize *Cephalanthus chinensis* Lam. as a *Breonia*. Noteworthy is that Ridsdale did not cite the type specimen of *N. citrifolia* Poir. Bosser (1984) disagreed with Capuron, arguing that an unnumbered Commerson collection from Madagascar in P-LA is the type specimen of *N. citrifolia* Poir. It is unclear whether Bosser referred to the Commerson *s.n.* in P-LA that serves as the type of *Cephalanthus chinensis* Lam. In any case, this does not correspond to the protologue of *N. citrifolia* Poir.

Despite Richard's statement (Richard, 1830: 210) that his *Cephalidium citrifolium* [= *Breonia chinensis*] was based on *Nauclea citrifolia* Poir., Bosser (1984) argued that the name *Cephalidium* was not based on the same type as *N. citrifolia* and therefore should be cited as *Cephalidium citrifolium* A. Rich. Also, Bosser further argued that the type specimen of *C. citrifolium* is another unnumbered collection of Commerson now in P. This Commerson *s.n.* at P collection is misidentified as *N. citrifolia* Poir., but it is actually a completely different species of *Breonia* I describe here as *B. taolagnaroensis*. This P collection of Commerson has fruit only, whereas both Poiret's protologue of *N. citrifolia* and Richard's protologue of *Cephalidium citrifolium* included flowers and fruits. Ridsdale (1975) treated *Cephalidium citrifolium* (Poir.) A. Richard under his *Breonia citrifolia* (Poir.) Ridsdale, but I here consider it as a synonym of *Breonia chinensis* (Lam.) Capuron.

Additional specimens examined. MADAGASCAR. **Antsiranana:** District Antalaha, Soahitra, "suivant le ruisseau Soahitra dans la vallée," *s.n.* SF (TEF); Ambohitralanana, 9982 RN (TEF); Andrakarana, 9238 SF (TEF); Maromandia, Forêt de Bero, 12447 SF (TEF); Ambodiazovola, Ampanavoana, Vinanivao, Forêt de Sahaenjika, Bernard 327 (MO, TAN); Canton Antafononana, Vi-

nanivao, Ampanavoana, Parc Masoala, Bernard 187 (MO, TAN); District Sambava, Canton Analamanara au Sud de Tsaratanana, between Sambava and Antsirabe-Nord, 27192 SF (TEF); [Unknown locality], *Vigreuse* 15418 (TAN). **Fianarantsoa:** District Farafangana, Karianga, Decary 5511 (PRE), Decary 5513 (P), Decary 5573 (PRE); Efatsy, Forêt d'Analazaha, 15381 SF (TEF); Canton Ivato, Forêt d'Analila, 16217 SF (TEF), 15495 SF (TEF); District Fort-Carnot, Canton Ifanirea, Forêt d'Analamarina, 15287 SF (TEF); Canton Tolongoina, Ambinanindrano, 5964 SF (TEF); Ambatomalama, 15518 SF (TEF); Canton Manampatrana, "exploitation forestière" Ahamode Ionilahy, 7155 SF (TEF); District Ifanadiana, Ranomafana National Park, between Morafeno and Sahavanana, Turk et al. 643 (MO, TAN); Canton Kianjavato, entre Ifanadiana et Anosivolo, 23917 SF (TEF); District Manakara, Forêt d'Andafa, 14728 SF (TEF); Forêt de Manakara au nord du terrain d'aviation, 86-R-118 (TEF); District Vohipeno, vestiges de forêt au Nord de Vohipeno, 23691 SF (TEF); Tsararano, 6360 SF (TEF); District Mananjary, Canton Anosimparihy, Manakana, 14437 SF (TEF); Canton Morafeno, Ambodinonoka, 16174 SF (TEF); Marofotra, Forêt de Mananjavara, 14712 SF (TEF); District Vaingaindrano, between Lopary and Vangaindrano, 23661 SF (TEF). **Toamasina:** District Brickaville, Managisy, 12352 SF (TEF); District Mahanoro, Canton d'Ambodinanidilana 1 km à l'Est d'Ambodiala, Forêt d'Amboagibe, 19658 SF (TEF); remnant native vegetation 1–2 km E of Fampanambo, Schatz et al. 3858 (MO, TAN); District Maroantsetra, Canton Andranofoy, Ambodikakazo au bord de la rivière d'Andranofotsy, 21596 SF (TEF); Baie d'Antongil, bassin de Rantabe, between Antsambalahy and Beanana, 9047 SF (TEF); Masoala National Park, Andrombazaha, Rahajaso et al. 747 (MO); District Soanierana Ivongo, 2410 SF (TEF); Toamasina II, Canton Ampan'Onive, Andranotsara, Mahatsara, 33240 SF (TEF), 34711 SF (TEF), 34719 SF (TEF); Ambodiriana, 17299 SF (TEF); Vohimarangitra, 31809 (TEF); Forêt d'Analalava à l'Ouest de Foulpointe, 28081 SF (TEF); District Vavatenina, Canton Sahatavy, Maizinandro, 26103 SF (TEF).

4. *Breonia cuspidata* (Baker) Haviland, J. Linn. Soc. Bot. 33: 37. 1897. *Nauclea cuspidata* Baker, J. Linn. Soc. Bot. 25: 319. 1890. TYPE: Madagascar. "North West" [without exact locality], Sep. 1887 (fl), Baron 5563 (holotype, K!).

Trees, height unknown. Bark with annular fissures. Leafy stems rounded, glabrous. Terminal vegetative buds conical, 4–5 × 1–1.2 mm, glabrous. Leaves persistent; petioles ca. 10–13 mm long, adaxially canaliculate, glabrous; blades 5.5–10 × 1.9–3 cm, oblanceolate, glabrous, membranaceous, glossy, apex caudate, base attenuate; margins glabrous, entire; secondary veins 8 to 9 pairs per side, eucamptodromous, adaxially inconspicuous, abaxially conspicuous; domatia absent; stipules ca. 5 mm long, cymbiform, not carinate, glabrous, free at the base, deciduous. Inflorescence solitary, heads ca. 2 cm wide; inflorescence axes 4.5–6.5 cm long, strongly flattened, slender, glabrous; bracts calyptra-like, deciduous; peduncles not present. Flowers 5-merous; calyx tubes ca. 1

name and number) with four labels in P-LA that may be the type of *N. citrifolia* Poir. The first label is Lamarck's and says: "*Nauclea citrifolia* dic n° 2." The second is Roeper's and states: "? 8. *Nauclea cadamba* Roxb.? [and] *Nauclea citrifolia* Poir.!!!, per quem affinis orientalis! immonimis affinis." The third states that this specimen returned to P-LA: Herbar de Lamarck, "acquis en Novembre 1886." The fourth label is that of Capuron and states: "*Breonia chinensis* (Lamk.) R. Capuron." Capuron (1973a) considered that this Lamarck specimen is the type of *Nauclea citrifolia* Poir. and is conspecific with *Breonia chinensis* (Lam.) Capuron. I concur with him because the protologue of *N. citrifolia* Poir. in Lamarck (1789: 435) agrees with this specimen. Ridsdale (1975) also endorsed Capuron's view, but made the new combination *Breonia citrifolia* (Poir.) Ridsdale because he did not recognize *Cephalanthus chinensis* Lam. as a *Breonia*. Noteworthy is that Ridsdale did not cite the type specimen of *N. citrifolia* Poir. Bosser (1984) disagreed with Capuron, arguing that an unnumbered Commerson collection from Madagascar in P-LA is the type specimen of *N. citrifolia* Poir. It is unclear whether Bosser referred to the *Commerson s.n.* in P-LA that serves as the type of *Cephalanthus chinensis* Lam. In any case, this does not correspond to the protologue of *N. citrifolia* Poir.

Despite Richard's statement (Richard, 1830: 210) that his *Cephalidium citrifolium* [= *Breonia chinensis*] was based on *Nauclea citrifolia* Poir., Bosser (1984) argued that the name *Cephalidium* was not based on the same type as *N. citrifolia* and therefore should be cited as *Cephalidium citrifolium* A. Rich. Also, Bosser further argued that the type specimen of *C. citrifolium* is another unnumbered collection of Commerson now in P. This *Commerson s.n.* at P collection is misidentified as *N. citrifolia* Poir., but it is actually a completely different species of *Breonia* I describe here as *B. taolagnaroensis*. This P collection of Commerson has fruit only, whereas both Poiret's protologue of *N. citrifolia* and Richard's protologue of *Cephalidium citrifolium* included flowers and fruits. Ridsdale (1975) treated *Cephalidium citrifolium* (Poir.) A. Richard under his *Breonia citrifolia* (Poir.) Ridsdale, but I here consider it as a synonym of *Breonia chinensis* (Lam.) Capuron.

Additional specimens examined. MADAGASCAR. **Antsiranana:** District Antalaha, Soahitra, "suivant le ruisseau Soahitra dans la vallée," *s.n.* SF (TEF); Ambohitralanana, 9982 RN (TEF); Andrakarana, 9238 SF (TEF); Maromandia, Forêt de Bero, 12447 SF (TEF); Ambodiazovola, Ampanavoana, Vinanivao, Forêt de Sahaenjika, Bernard 327 (MO, TAN); Canton Antafononana, Vi-

nanivao, Ampanavoana, Parc Masoala, Bernard 187 (MO, TAN); District Sambava, Canton Analamanara au Sud de Tsaratanana, between Sambava and Antsirabe-Nord, 27192 SF (TEF); [Unknown locality], *Vigreuse 15418* (TAN). **Fianarantsoa:** District Farafangana, Karianga, Decary 5511 (PRE), Decary 5513 (P), Decary 5573 (PRE); Efatsy, Forêt d'Analazaha, 15381 SF (TEF); Canton Ivato, Forêt d'Analila, 16217 SF (TEF), 15495 SF (TEF); District Fort-Carnot, Canton Ifanirea, Forêt d'Analamarina, 15287 SF (TEF); Canton Tolongoina, Ambinanindrano, 5964 SF (TEF); Ambatomalama, 15518 SF (TEF); Canton Manampatrana, "exploitation forestière" Ahamode Ionilahy, 7155 SF (TEF); District Ifanadiana, Ranomafana National Park, between Morafeno and Sahavanana, Turk et al. 643 (MO, TAN); Canton Kianjavato, entre Ifanadiana et Anosivolo, 23917 SF (TEF); District Manakara, Forêt d'Andafa, 14728 SF (TEF); Forêt de Manakara au nord du terrain d'aviation, 86-R-118 (TEF); District Vohipeno, vestiges de forêt au Nord de Vohipeno, 23691 SF (TEF); Tsararano, 6360 SF (TEF); District Mananjary, Canton Anosimparihy, Manakana, 14437 SF (TEF); Canton Morafeno, Ambodinonoka, 16174 SF (TEF); Marofotra, Forêt de Mananjavara, 14712 SF (TEF); District Vaingaindrano, between Lopary and Vangaindrano, 23661 SF (TEF). **Toamasina:** District Brickaville, Managisy, 12352 SF (TEF); District Mahanoro, Canton d'Ambodinanidilana 1 km à l'Est d'Ambodiala, Forêt d'Amboagibe, 19658 SF (TEF); remnant native vegetation 1–2 km E of Fampanambo, Schatz et al. 3858 (MO, TAN); District Maroantsetra, Canton Andranofoy, Ambodikakazo au bord de la rivière d'Andranofotsy, 21596 SF (TEF); Baie d'Antongil, bassin de Rantabe, between Antsambalahy and Beanana, 9047 SF (TEF); Masoala National Park, Andrombazaha, Rahajaso et al. 747 (MO); District Soanierana Ivongo, 2410 SF (TEF); Toamasina II, Canton Ampan'Onive, Andranotsara, Mahatsara, 33240 SF (TEF), 34711 SF (TEF), 34719 SF (TEF); Ambodiriana, 17299 SF (TEF); Vohimarangitra, 31809 (TEF); Forêt d'Analalava à l'Ouest de Foulpointe, 28081 SF (TEF); District Vavatenina, Canton Sahatavy, Maizinandro, 26103 SF (TEF).

4. *Breonia cuspidata* (Baker) Haviland, J. Linn. Soc. Bot. 33: 37. 1897. *Nauclea cuspidata* Baker, J. Linn. Soc. Bot. 25: 319. 1890. TYPE: Madagascar. "North West" [without exact locality], Sep. 1887 (fl), Baron 5563 (holotype, K!).

Trees, height unknown. Bark with annular fissures. Leafy stems rounded, glabrous. Terminal vegetative buds conical, 4–5 × 1–1.2 mm, glabrous. Leaves persistent; petioles ca. 10–13 mm long, adaxially canaliculate, glabrous; blades 5.5–10 × 1.9–3 cm, oblanceolate, glabrous, membranaceous, glossy, apex caudate, base attenuate; margins glabrous, entire; secondary veins 8 to 9 pairs per side, eucamptodromous, adaxially inconspicuous, abaxially conspicuous; domatia absent; stipules ca. 5 mm long, cymbiform, not carinate, glabrous, free at the base, deciduous. Inflorescence solitary, heads ca. 2 cm wide; inflorescence axes 4.5–6.5 cm long, strongly flattened, slender, glabrous; bracts calyptra-like, deciduous; peduncles not present. Flowers 5-merous; calyx tubes ca. 1

mm long, free, inside lanate, outside up to the middle glabrous, above the middle lanate; lobes ca. 0.2 mm long, triangular, lanate; corolla tubes ca. 5×0.8 – 0.9 mm; lobes 1.1–1.3 mm long, broadly oblong, glabrous; anthers 0.7–0.8 mm long, filaments 0.2–0.3 mm long; styles 8–9 mm long; stigmas clavate to capitate; ovary 2-carpellate; carpels syncarpous; ovule 1 per locule, pendulous; placentae reduced, pendulous. Infructescences not seen.

Distribution and habitat. Northwest Madagascar; habitats unknown.

Common names. Unknown.

Phenology. Flowering September; fruiting time unknown.

Discussion. *Breonia cuspidata* appears to have a restricted distribution and has not been collected since 1890. This species is distinguished from the other species by its ovaries with one ovule per locule and its leaf blades with caudate apices and attenuate bases.

Original paratypes. [Unknown locality], *Baron 6602* (K!) and *Scott Elliott 2214* (K!).

5. *Breonia decaryana* Homolle, Bull. Soc. Bot. France 84: 460. 1937 [publ. 1938]. *Neobreonia decaryana* (Homolle) Ridsdale, Blumea 22: 546. 1975. TYPE: Madagascar. [Fianarantsoa province], District Farafangana, Ifandana, *Decary 5199* (holotype, P!; isotype, L not seen). Figures 1A and 2A.

Breonia keliravina Homolle, Bull. Soc. Bot. France 84: 460. 1937 [publ. 1938]. TYPE: Madagascar. Analamazaotra, *Thouvenot 91* (lectotype, designated by Ridsdale (1975: 546), P!).

Trees, 10–30 m tall. Bark rugose with annular fissures, rarely smooth, lenticellate. Leafy stems quadrangular, glabrous, always dichotomously branched. Terminal vegetative buds complanate, 8 – 14×6 – 10 mm, glabrous. Leaves persistent; petioles 10 – 20×2 – 3 mm, adaxially canaliculate, glabrous; leaf blades (4) – 6.5 – $12 \times (1.5)$ – 3 – 7.5 cm, oblanceolate to broadly obovate or broadly elliptic, glabrous, coriaceous, glossy, apex rounded to broadly cuspidate, base cuneate to attenuate, or rounded; margins glabrous, entire; secondary veins (6 or 7) to 10 pairs per side, eucamptodromous, adaxially inconspicuous, abaxially conspicuous; domatia absent; stipules 10–14 mm long, ovate to obovate, abaxially carinate, glabrous, free at the base, deciduous. Inflorescences 4 to 8 per axil; heads 1.5–1.8 cm wide; inflorescence axes 2.8–5 cm long, terete or slightly flattened; bracts calyptra-like, persistent; peduncles 0.8–2 cm long, sparsely pubescent. Flowers 4-merous; calyx tubes ca. 1 mm

long, completely fused, lobes ca. 1 mm long, inside and outside densely pubescent; corolla tubes ca. 4×1 mm, red, glabrous, lobes ca. 1 mm long, broadly oblong, yellow-tinged, glabrous; anthers ca. 1 mm long. Styles 7 – 8×1 – 1.5 mm; stigmas globose; ovary 2-carpellate; carpel coherent; ovule 1 per locule, pendulous; placentae small. Infructescences 0.5–1.7 cm diam., rugose, with calyx remnants barely evident; individual fruits with endocarp hard, glossy; disks accrescent, rounded, deeply divided; seed 1 per locule, strongly flattened, red; seed-coat lineate.

Habitat and distribution. Evergreen rainforests, occasionally in riverbeds; Districts of Andapa, Moramanga, and Farafangana (Fig. 7).

Common names. Molompangady keliravina, Marotsaka, Valompangady, Valotro, and Valotsy.

Phenology. Flowering May to August; fruiting September to February.

Discussion. *Breonia decaryana* can easily be distinguished from the rest of the *Breonia* species by its complanate terminal vegetative buds and 4 to 8 inflorescences per axil. This species was removed by Ridsdale from *Breonia* simply because it has flattened terminal vegetative buds and partly fused corolla tubes. I here include it in *Breonia* because this species shares one morphological synapomorphy with *Breonia* sensu Ridsdale (large accrescent disks); additionally, they all have multiple fruits. I endorsed Ridsdale's decision on sinking *B. keliravina* in *B. decaryana* because the former has all the diagnostic features of the latter. The specimen *Louvel 216* (P!) was one of the two cited by Homolle (1938) in the protologue of *B. keliravina*.

Additional specimens examined. MADAGASCAR. **Antsiranana:** District Andapa, Réserve Spéciale d'Anjanaharibe-Sud, *Razafimandimbison SG 257* (MO, TAN). **Toamasina:** District Moramanga, Canton Analamazaotra, *Thouvenot s.n.* (P), *Louvel 216* (P); Ambodivoasary, *12-B-R-172* (TEF); Anosibe, *26804 SF* (TEF), *28414 SF* (TEF), *28445 SF* (TEF).

6. *Breonia fragifera* Capuron ex Razafim., sp. nov. TYPE: Madagascar. Antsiranana province: District Antalaha, Canton Ampanavoana, Antsiramoranga, 6 Dec. 1954 (fl), *6809 RN* (holotype, TEF). Figures 2C and 9.

Haec species a congeneris disco nectarifero accrescente permagno atque fructu pustulato distinguitur.

Shrubs, spreading shrubs, or trees, 5–15 m tall. Bark rugose. Leafy stems terete, glabrous. Terminal vegetative buds conical, 3 – $3.5 \times$ ca. 3 mm, glabrous. Leaves persistent; petioles 25 – $70 \times$ ca. 1.5 mm, terete, glabrous; blades 8 – 13×2.2 – 4 (– 6.5)

mm long, free, inside lanate, outside up to the middle glabrous, above the middle lanate; lobes ca. 0.2 mm long, triangular, lanate; corolla tubes ca. 5×0.8 – 0.9 mm; lobes 1.1–1.3 mm long, broadly oblong, glabrous; anthers 0.7–0.8 mm long, filaments 0.2–0.3 mm long; styles 8–9 mm long; stigmas clavate to capitate; ovary 2-carpellate; carpels syncarpous; ovule 1 per locule, pendulous; placentae reduced, pendulous. Infructescences not seen.

Distribution and habitat. Northwest Madagascar; habitats unknown.

Common names. Unknown.

Phenology. Flowering September; fruiting time unknown.

Discussion. *Breonia cuspidata* appears to have a restricted distribution and has not been collected since 1890. This species is distinguished from the other species by its ovaries with one ovule per locule and its leaf blades with caudate apices and attenuate bases.

Original paratypes. [Unknown locality], *Baron 6602* (K!) and *Scott Elliott 2214* (K!).

5. *Breonia decaryana* Homolle, Bull. Soc. Bot. France 84: 460. 1937 [publ. 1938]. *Neobreonia decaryana* (Homolle) Ridsdale, Blumea 22: 546. 1975. TYPE: Madagascar. [Fianarantsoa province], District Farafangana, Ifandana, *Decary 5199* (holotype, P!; isotype, L not seen). Figures 1A and 2A.

Breonia keliravina Homolle, Bull. Soc. Bot. France 84: 460. 1937 [publ. 1938]. TYPE: Madagascar. Analamazaotra, *Thouvenot 91* (lectotype, designated by Ridsdale (1975: 546), P!).

Trees, 10–30 m tall. Bark rugose with annular fissures, rarely smooth, lenticellate. Leafy stems quadrangular, glabrous, always dichotomously branched. Terminal vegetative buds complanate, 8 – 14×6 – 10 mm, glabrous. Leaves persistent; petioles 10 – 20×2 – 3 mm, adaxially canaliculate, glabrous; leaf blades (4) – 6.5 – $12 \times (1.5)$ – 3 – 7.5 cm, oblanceolate to broadly obovate or broadly elliptic, glabrous, coriaceous, glossy, apex rounded to broadly cuspidate, base cuneate to attenuate, or rounded; margins glabrous, entire; secondary veins (6 or 7) to 10 pairs per side, eucamptodromous, adaxially inconspicuous, abaxially conspicuous; domatia absent; stipules 10–14 mm long, ovate to obovate, abaxially carinate, glabrous, free at the base, deciduous. Inflorescences 4 to 8 per axil; heads 1.5–1.8 cm wide; inflorescence axes 2.8–5 cm long, terete or slightly flattened; bracts calyptra-like, persistent; peduncles 0.8–2 cm long, sparsely pubescent. Flowers 4-merous; calyx tubes ca. 1 mm

long, completely fused, lobes ca. 1 mm long, inside and outside densely pubescent; corolla tubes ca. 4×1 mm, red, glabrous, lobes ca. 1 mm long, broadly oblong, yellow-tinged, glabrous; anthers ca. 1 mm long. Styles 7 – 8×1 – 1.5 mm; stigmas globose; ovary 2-carpellate; carpel coherent; ovule 1 per locule, pendulous; placentae small. Infructescences 0.5–1.7 cm diam., rugose, with calyx remnants barely evident; individual fruits with endocarp hard, glossy; disks accrescent, rounded, deeply divided; seed 1 per locule, strongly flattened, red; seed-coat lineate.

Habitat and distribution. Evergreen rainforests, occasionally in riverbeds; Districts of Andapa, Moramanga, and Farafangana (Fig. 7).

Common names. Molompangady keliravina, Marotsaka, Valompangady, Valotro, and Valotsy.

Phenology. Flowering May to August; fruiting September to February.

Discussion. *Breonia decaryana* can easily be distinguished from the rest of the *Breonia* species by its complanate terminal vegetative buds and 4 to 8 inflorescences per axil. This species was removed by Ridsdale from *Breonia* simply because it has flattened terminal vegetative buds and partly fused corolla tubes. I here include it in *Breonia* because this species shares one morphological synapomorphy with *Breonia* sensu Ridsdale (large accrescent disks); additionally, they all have multiple fruits. I endorsed Ridsdale's decision on sinking *B. keliravina* in *B. decaryana* because the former has all the diagnostic features of the latter. The specimen *Louvel 216* (P!) was one of the two cited by Homolle (1938) in the protologue of *B. keliravina*.

Additional specimens examined. MADAGASCAR. **Antsiranana:** District Andapa, Réserve Spéciale d'Anjanaharibe-Sud, *Razafimandimbison SG 257* (MO, TAN). **Toamasina:** District Moramanga, Canton Analamazaotra, *Thouvenot s.n.* (P), *Louvel 216* (P); Ambodivoasary, *12-B-R-172* (TEF); Anosibe, *26804 SF* (TEF), *28414 SF* (TEF), *28445 SF* (TEF).

6. *Breonia fragifera* Capuron ex Razafim., sp. nov. TYPE: Madagascar. Antsiranana province: District Antalaha, Canton Ampanavoana, Antsiramoranga, 6 Dec. 1954 (fl), *6809 RN* (holotype, TEF). Figures 2C and 9.

Haec species a congeneris disco nectarifero accrescente permagno atque fructu pustulato distinguitur.

Shrubs, spreading shrubs, or trees, 5–15 m tall. Bark rugose. Leafy stems terete, glabrous. Terminal vegetative buds conical, 3 – $3.5 \times$ ca. 3 mm, glabrous. Leaves persistent; petioles 25 – $70 \times$ ca. 1.5 mm, terete, glabrous; blades 8 – 13×2.2 – 4 (– 6.5)

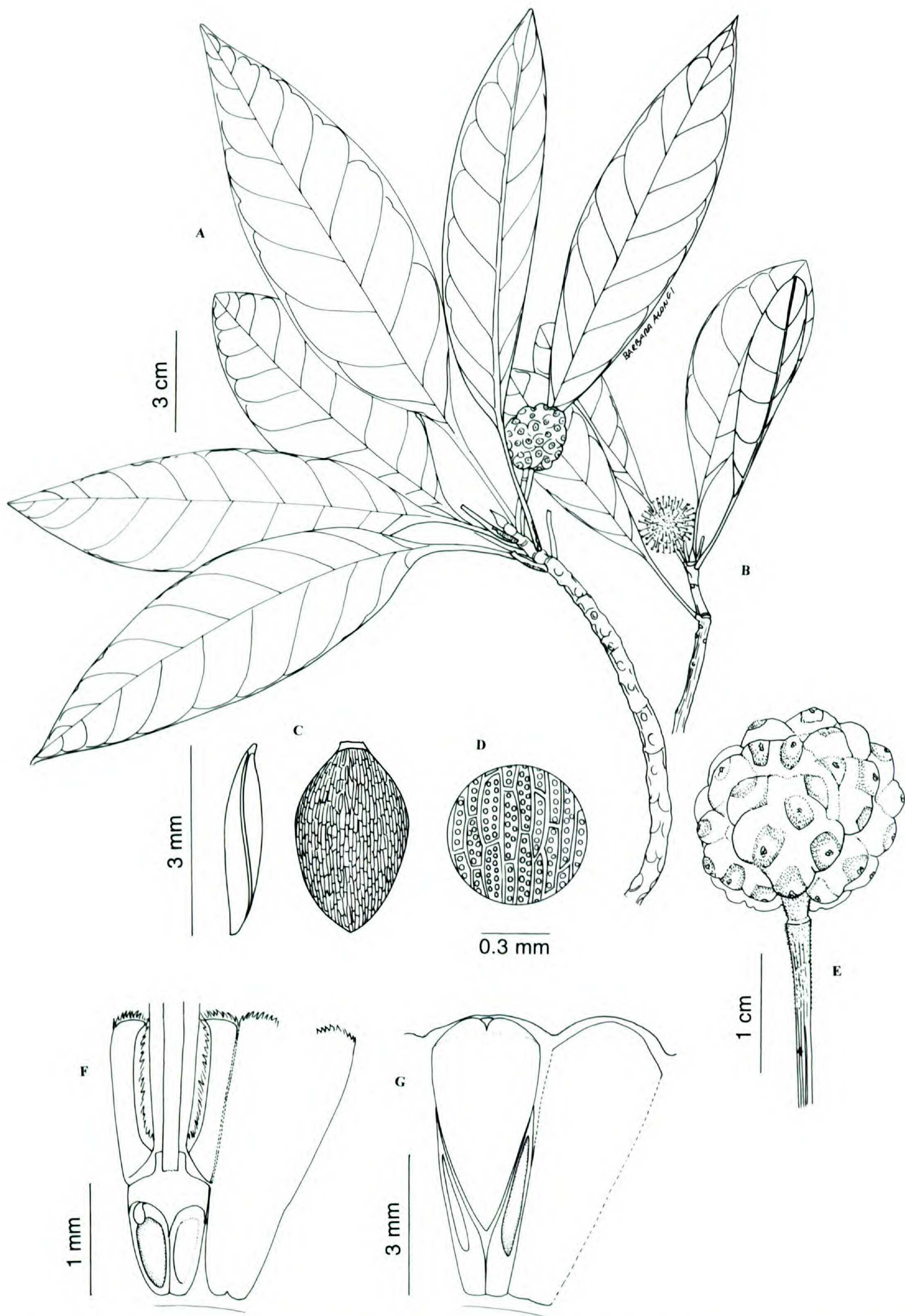


Figure 9. *Breonia fragifera*.—A. Fertile branch with mature infructescence. —B. Fertile branch with inflorescence. —C. Seed, showing flattened lateral profile (left); dorsal view (right). —D. Seed-coat texture. —E. Mature infructescence. —F. Median dissection through flower, showing velutinous calyx tube and unicarpellate ovary with single pen-

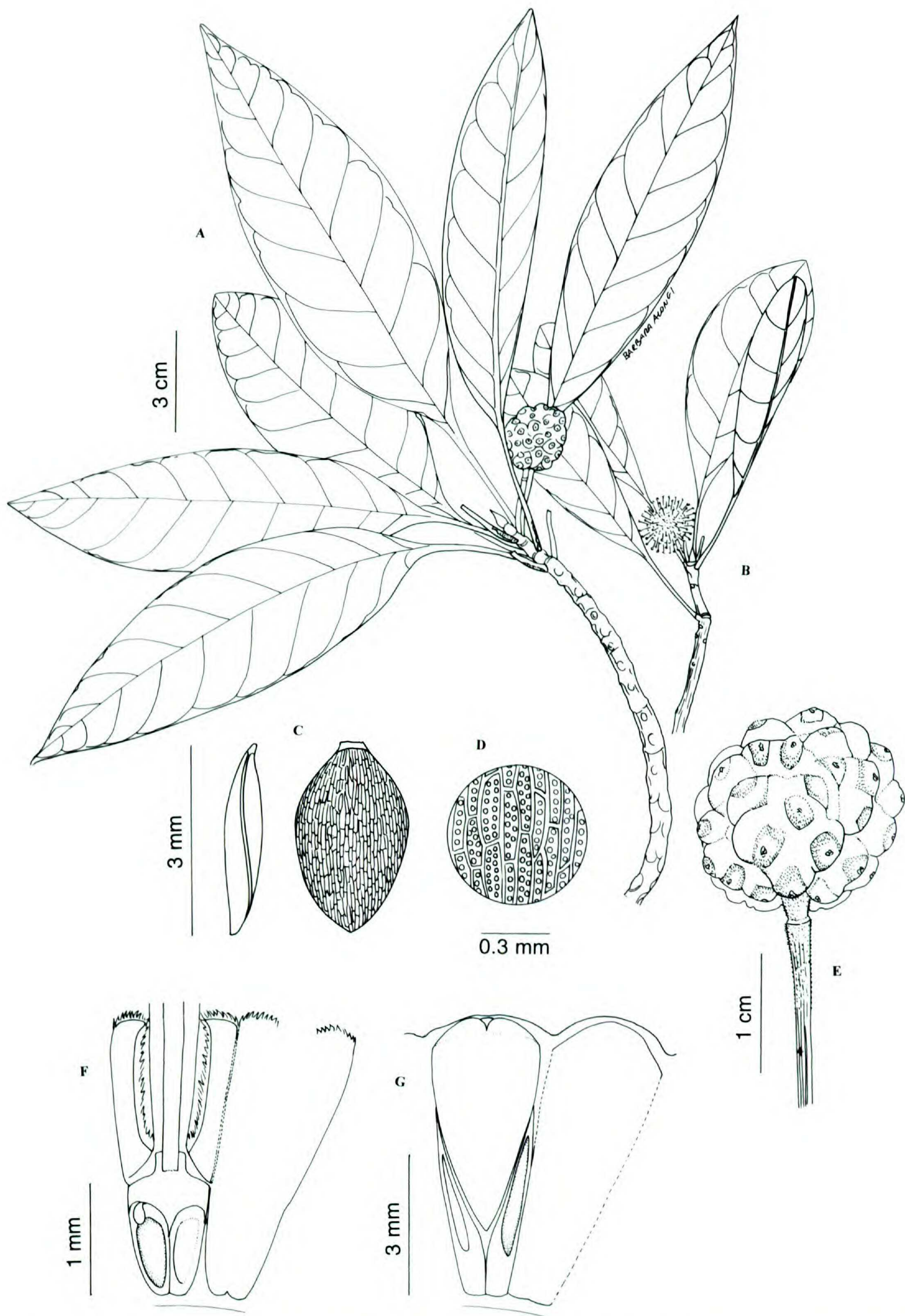


Figure 9. *Breonia fragifera*.—A. Fertile branch with mature infructescence. —B. Fertile branch with inflorescence. —C. Seed, showing flattened lateral profile (left); dorsal view (right). —D. Seed-coat texture. —E. Mature infructescence. —F. Median dissection through flower, showing velvinous calyx tube and unicarpellate ovary with single pen-

cm, oblanceolate to ovate, glabrous, coriaceous or membranaceous, glossy, apex cuspidate to acute, base cuneate; margin glabrous, entire; secondary veins 7 to 9 pairs per side, eucamptodromous; domatia absent; stipules ca. 3×2 mm, cymbiform, not carinate, glabrous, free at the base, deciduous. Inflorescences solitary; heads 1.5–2 cm wide; inflorescence axes 1.2–3.5 cm long, terete; bracts calyptra-like, deciduous; peduncles 2–3 mm long. Flowers mostly 4-merous; calyx tubes ca. 0.5 mm long, velutinous, lobes lanate; corolla tubes ca. 4×1 mm, white-tinged, glabrous; lobes ca. 1 mm long, oblong, ciliate or glabrous; anthers ca. 0.5 mm long; filaments ca. 0.1 mm long, glabrous, terete; styles ca. 7×0.2 mm, glabrous; stigmas capitate; ovary 2-carpellate; carpels coherent; ovules 1 per locule, pendulous. Infructescences 1.6–2 cm diam., pusticulate, with calyx remnant barely evident; individual fruits with endocarp soft, fibrous; disks accrescent, massive, obtriangular; seed 1 per locule, strongly flattened, ellipsoid, red; seed-coat lineate.

Habitat and distribution. Low-altitude forests; Districts of Ambanja, Antalaha, Fort-Carnot, Toamasina II, Fort-Dauphin (Fig. 7).

Common names. Valotra, Valotralahy (male Valotra).

Phenology. Flowering November–March; fruiting June to March.

Discussion. This species is diagnosed by its massive, accrescent disks and pusticulate fruits. It was lumped by Ridsdale (1975) in *Breonia sphaerantha*. The species name was taken from the labels of the herbarium specimens of *Breonia fragifera* received from TEF. The epithet “*fragifera*” indicates strawberries-bearing, referring to its inflorescences.

Paratypes. MADAGASCAR. **Antsiranana:** District Ambanja, *Randrianaivo* 251 (MO); Beampangibe, 2961 SF (TEF); Besinkara, Ambalafary, *Gautier et al.* 3288 (K, MO); Canton Marovato, Mahalina, 7460 SF (TEF); Presqu’île d’Ambato, forêt classée, *Antilahimena et al.* 324 (MO); District Antalaha, Canton Ampahana, Andranomadio, 21570 SF (TEF). **Fianarantsoa:** District Fort-Carnot, Canton Ifanirea, 19791 SF (TEF), 19775 SF (TEF). **Toamasina:** Ambodiriana 9045 RN (TEF); environs de la Baie d’Antongil, Massif d’Antsirosiro, 8734 SF (TEF); Toamasina II, Ampasimbe, Andranotsara, SFF Mahatsara, *Comtet* 33237 SF (TEF), *Comtet* 33536 SF (TEF), *Comtet* 34288 SF (TEF), *Comtet* 34413 SF (TEF), *Noyes et al.* 961 (K, MO, P, TAN); Réserve Naturelle Intégrale de Betampona, piste Sahafoza, *Andrianarisata et al.* 259 (TAN). **Toliara:** District Fort-Dauphin, 5152 RN (P, TEF), *Randriamampionona* 438 (MO); Canton Ifarant-

sa, Antsako, 10803 SF (TEF); Isaka-Ivondro au bords de la rivière Kovazaza, 11503 SF (TEF).

7. *Breonia havilandiana* Homolle, Bull. Soc. Bot. Fr. 84: 464. 1937 [publ. 1938]. TYPE: Madagascar. [Fianarantsoa province], “bords de l’Anosivola (Mangoro),” 700 m, Sep. 1911 (fl), *Perrier de la Bâthie* 3904 (holotype, P!).

Trees, 10–20 m tall. Bark fissured longitudinally. Leafy stems glabrous, lenticellate. Terminal vegetative buds conical, $15\text{--}19 \times 3.5\text{--}4$ mm, glabrous. Leaves deciduous; petioles $15\text{--}25 \times$ ca. 2 mm, terete, glabrous; blades $8\text{--}19(\text{--}21) \times 5\text{--}9(\text{--}12)$ cm, obovate, always rippled or wavy when dry, glabrous, coriaceous, apex obtuse to rounded, base cuneate; margins glabrous, entire; secondary veins 8 to 10 pairs per side, eucamptodromous, abaxially prominent; ciliate-type domatia; stipules ca. 20×3 mm, cymbiform, abaxially carinate, glabrous, free at the base, deciduous. Inflorescence solitary, rarely 2 per axil, heads ca. 2.3–2.9 cm wide; bracts calyptra-like; inflorescence axes 3–4 cm long, glabrous; peduncles ca. 3–4 mm long, glabrous. Flowers 5-merous; calyx tubes ca. 3.5 mm long, inside at the base velutinous, toward the lobes pubescent, outside glabrous, a few straight long hairs surrounding the base, lobes oblong, tomentose; corolla tubes ca. $5 \times 0.6\text{--}0.7$ mm, glabrous, lobes 1.5–2.5 mm long, oblong; anthers 1.1–1.2 mm long; filaments ca. 0.1 mm long, glabrous, flattened; styles $8.5\text{--}9 \times$ ca. 0.2 mm, glabrous; stigmas capitate, shallowly bifid; ovary 2-carpellate; carpels syncarpous; ovules 2 to 4 per locule, flattened, pendulous, imbricate; placentae flattened, elongated. Infructescence 1.7–2.5 cm diam., with well-developed calyx remnants; individual fruits with endocarp soft, not glossy; disks accrescent, obconical; seeds 2 to 4 per locule, strongly flattened, ellipsoid, red; seed-coat reticulate.

Habitat and distribution. Low- and mid-altitude evergreen rainforests; Districts of Ifanadiana, Befandriana-Nord, Moramanga, Fort-Carnot, and Anosibe an’Ala (Fig. 5).

Common names. Molompangady, Molotr’angady (lips of spade), Mamalifangady.

Phenology. Flowering October to November; fruiting September to January.

Discussion. This species is distinctive in having leaf blades that are undulate when dry.

Additional specimens examined. MADAGASCAR.

←

dulous ovule each (left); entire flower (right). —G. Median dissection through infructescence revealing massive disk and uniovulate carpels (left); entire fruit (right). A, B, F from 6809 RN (TEF) and C–E, G from 19775 SF (TEF).

cm, oblanceolate to ovate, glabrous, coriaceous or membranaceous, glossy, apex cuspidate to acute, base cuneate; margin glabrous, entire; secondary veins 7 to 9 pairs per side, eucamptodromous; domatia absent; stipules ca. 3×2 mm, cymbiform, not carinate, glabrous, free at the base, deciduous. Inflorescences solitary; heads 1.5–2 cm wide; inflorescence axes 1.2–3.5 cm long, terete; bracts calyptra-like, deciduous; peduncles 2–3 mm long. Flowers mostly 4-merous; calyx tubes ca. 0.5 mm long, velutinous, lobes lanate; corolla tubes ca. 4×1 mm, white-tinged, glabrous; lobes ca. 1 mm long, oblong, ciliate or glabrous; anthers ca. 0.5 mm long; filaments ca. 0.1 mm long, glabrous, terete; styles ca. 7×0.2 mm, glabrous; stigmas capitate; ovary 2-carpellate; carpels coherent; ovules 1 per locule, pendulous. Infructescences 1.6–2 cm diam., pusticulate, with calyx remnant barely evident; individual fruits with endocarp soft, fibrous; disks accrescent, massive, obtriangular; seed 1 per locule, strongly flattened, ellipsoid, red; seed-coat lineate.

Habitat and distribution. Low-altitude forests; Districts of Ambanja, Antalaha, Fort-Carnot, Toamasina II, Fort-Dauphin (Fig. 7).

Common names. Valotra, Valotralahy (male Valotra).

Phenology. Flowering November–March; fruiting June to March.

Discussion. This species is diagnosed by its massive, accrescent disks and pusticulate fruits. It was lumped by Ridsdale (1975) in *Breonia sphaerantha*. The species name was taken from the labels of the herbarium specimens of *Breonia fragifera* received from TEF. The epithet “*fragifera*” indicates strawberries-bearing, referring to its inflorescences.

Paratypes. MADAGASCAR. **Antsiranana:** District Ambanja, *Randrianaivo* 251 (MO); Beampangibe, 2961 SF (TEF); Besinkara, Ambalafary, *Gautier et al.* 3288 (K, MO); Canton Marovato, Mahalina, 7460 SF (TEF); Presqu’île d’Ambato, forêt classée, *Antilahimena et al.* 324 (MO); District Antalaha, Canton Ampahana, Andranomadio, 21570 SF (TEF). **Fianarantsoa:** District Fort-Carnot, Canton Ifanirea, 19791 SF (TEF), 19775 SF (TEF). **Toamasina:** Ambodiriana 9045 RN (TEF); environs de la Baie d’Antongil, Massif d’Antsirosiro, 8734 SF (TEF); Toamasina II, Ampasimbe, Andranotsara, SFF Mahatsara, *Comtet* 33237 SF (TEF), *Comtet* 33536 SF (TEF), *Comtet* 34288 SF (TEF), *Comtet* 34413 SF (TEF), *Noyes et al.* 961 (K, MO, P, TAN); Réserve Naturelle Intégrale de Betampona, piste Sahafoza, *Andrianarisata et al.* 259 (TAN). **Toliara:** District Fort-Dauphin, 5152 RN (P, TEF), *Randriamampionona* 438 (MO); Canton Ifarant-

sa, Antsako, 10803 SF (TEF); Isaka-Ivondro au bords de la rivière Kovazaza, 11503 SF (TEF).

7. ***Breonia havilandiana*** Homolle, Bull. Soc. Bot. Fr. 84: 464. 1937 [publ. 1938]. TYPE: Madagascar. [Fianarantsoa province], “bords de l’Anosivola (Mangoro),” 700 m, Sep. 1911 (fl), *Perrier de la Bâthie* 3904 (holotype, P!).

Trees, 10–20 m tall. Bark fissured longitudinally. Leafy stems glabrous, lenticellate. Terminal vegetative buds conical, $15\text{--}19 \times 3.5\text{--}4$ mm, glabrous. Leaves deciduous; petioles $15\text{--}25 \times$ ca. 2 mm, terete, glabrous; blades $8\text{--}19(21) \times 5\text{--}9(12)$ cm, obovate, always rippled or wavy when dry, glabrous, coriaceous, apex obtuse to rounded, base cuneate; margins glabrous, entire; secondary veins 8 to 10 pairs per side, eucamptodromous, abaxially prominent; ciliate-type domatia; stipules ca. 20×3 mm, cymbiform, abaxially carinate, glabrous, free at the base, deciduous. Inflorescence solitary, rarely 2 per axil, heads ca. 2.3–2.9 cm wide; bracts calyptra-like; inflorescence axes 3–4 cm long, glabrous; peduncles ca. 3–4 mm long, glabrous. Flowers 5-merous; calyx tubes ca. 3.5 mm long, inside at the base velutinous, toward the lobes pubescent, outside glabrous, a few straight long hairs surrounding the base, lobes oblong, tomentose; corolla tubes ca. $5 \times 0.6\text{--}0.7$ mm, glabrous, lobes 1.5–2.5 mm long, oblong; anthers 1.1–1.2 mm long; filaments ca. 0.1 mm long, glabrous, flattened; styles $8.5\text{--}9 \times$ ca. 0.2 mm, glabrous; stigmas capitate, shallowly bifid; ovary 2-carpellate; carpels syncarpous; ovules 2 to 4 per locule, flattened, pendulous, imbricate; placentae flattened, elongated. Infructescence 1.7–2.5 cm diam., with well-developed calyx remnants; individual fruits with endocarp soft, not glossy; disks accrescent, obconical; seeds 2 to 4 per locule, strongly flattened, ellipsoid, red; seed-coat reticulate.

Habitat and distribution. Low- and mid-altitude evergreen rainforests; Districts of Ifanadiana, Befandriana-Nord, Moramanga, Fort-Carnot, and Anosibe an’Ala (Fig. 5).

Common names. Molompangady, Molotr’angady (lips of spade), Mamalifangady.

Phenology. Flowering October to November; fruiting September to January.

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Additional specimens examined. MADAGASCAR.

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dulous ovule each (left); entire flower (right). —G. Median dissection through infructescence revealing massive disk and uniovulate carpels (left); entire fruit (right). A, B, F from 6809 RN (TEF) and C–E, G from 19775 SF (TEF).

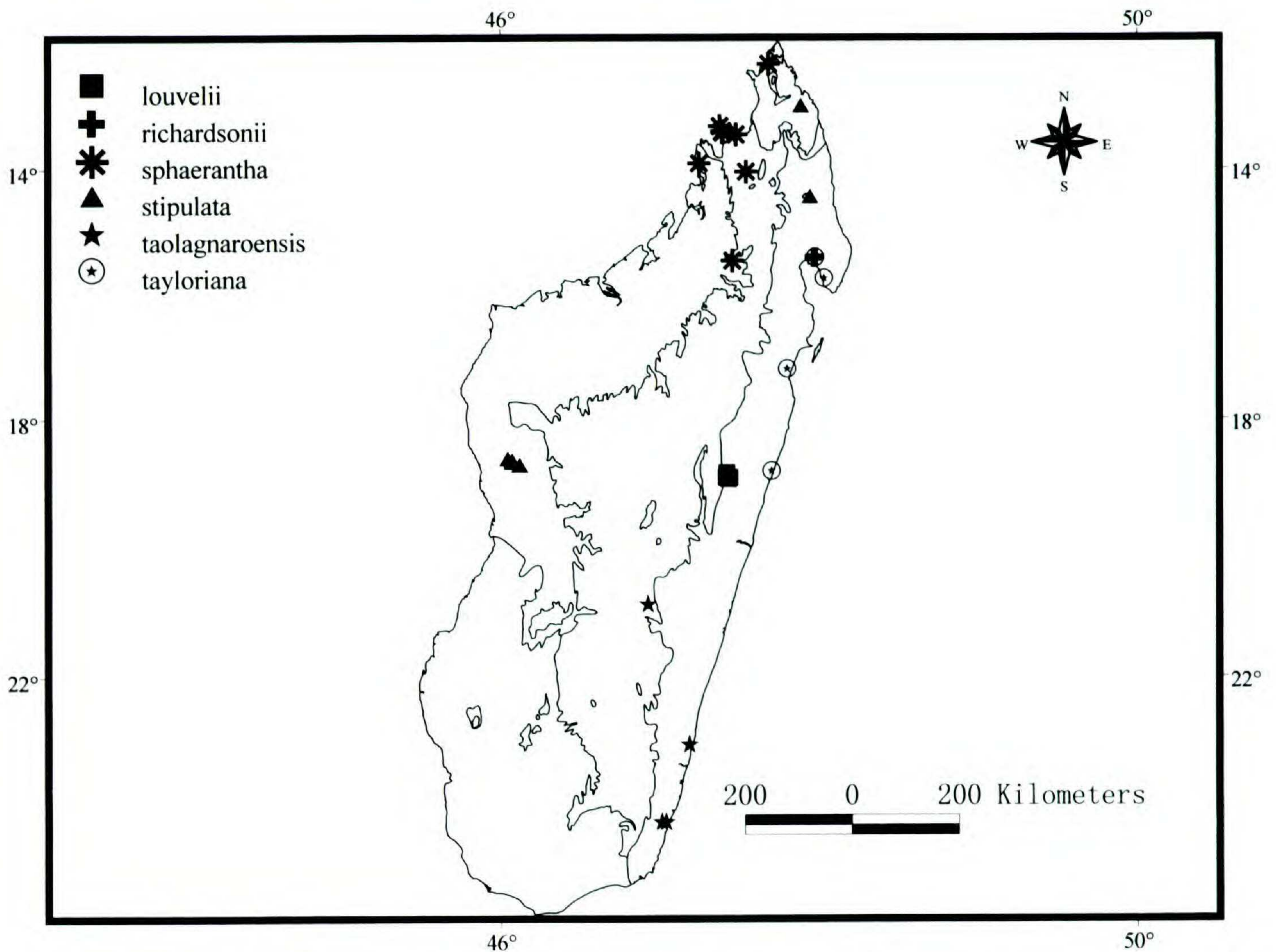


Figure 10. Distribution of *Breonia louvelii*, *B. richardsonii*, *B. sphaerantha*, *B. stipulata*, *B. taolagnaroensis*, and *B. tayloriana*.

Fianarantsoa: District Fort-Carnot, Canton Tolongoina, Ankadilalana, 19295 SF (TEF); Forêt d'Ambatoharanana, 7136 SF (TEF); District Ifanadiana, Ranomafana National Park, *Randrianasolo & Rasabotsy* 32 (MO), 9974 SF (TEF), *Razafimandimbison* SG 389 (MO, TAN). **Mahajanga:** District Befandriana-Nord, Canton Matsondakana, Belalona, Réserve Spéciale d'Anjanaharibe-Sud, *Ravelonarivo & Rabesaonina* 570 (MO). **Toamasina:** District Anosibe an'Ala, Tsaratampona, Mangorobilika, 25526 SF (TEF); District Moramanga, Canton Périnet, Sahamaloto, 6105 SF (TEF).

8. *Breonia louvelii* Homolle, Bull. Soc. Bot. France 84: 461. 1937 [publ. 1938]. TYPE: Madagascar. [Toamasina province], Analama-zotra, Sep. 1925 (fl), *Louvel* 125 (holotype, P!).

Medium-sized trees, 7–10 m tall. Bark with longitudinal fissures. Leafy stems rounded, glabrous, lenticellate. Terminal vegetative buds conical, 5–9 × 1–1.5 mm long, glabrous. Leaves persistent; petioles ca. 7–17 mm long, adaxially canaliculate, glabrous; blades ca. 4–9 × 1.5–3.5 cm, oblanceolate to elliptic, glabrous, coriaceous, glossy, apex acuminate to obtuse, base attenuate; margins glabrous, entire, slightly involute when dry; secondary veins 10 to 11 pairs per side, eucamptodromous, adaxi-

ally inconspicuous, abaxially conspicuous; domatia absent; stipules 5–9 × 1.5–1.8 mm, cymbiform, not carinate, glabrous, free at the base, deciduous. Inflorescence solitary, heads 1.8–2 cm wide; inflorescence axes 2–4 cm long, flattened, slender, glabrous; bracts calyptra-like, deciduous; peduncles ca. 2 mm long, glabrous. Flowers 5-merous or rarely 6-merous; calyx tubes ca. 1 mm long, free, lobes ca. 1 mm long, inside lanate, outside glabrous, lobes densely pubescent, truncate to oblong; corolla tubes 5–6 × 1–1.2 mm, glabrous, lobes 2–3 mm long, broadly oblong; anthers 1–1.5 mm long; filaments 0.2–0.3 mm long; styles 7–8 × 1–1.5 mm; stigmas capitate (shallowly bifid); ovary 2-carpellate; carpels syncarpous; ovule 1 per locule, pendulous; placentae small. Infructescences not seen.

Habitat and distribution. Evergreen rainforests; District of Moramanga (Fig. 10).

Common names. Hazomarotsaka (slender but tall trees), Molompanyady.

Phenology. Flowering September to October; fruiting December to January.

Discussion. This species has a very restricted geographical distribution and appears to be rare.

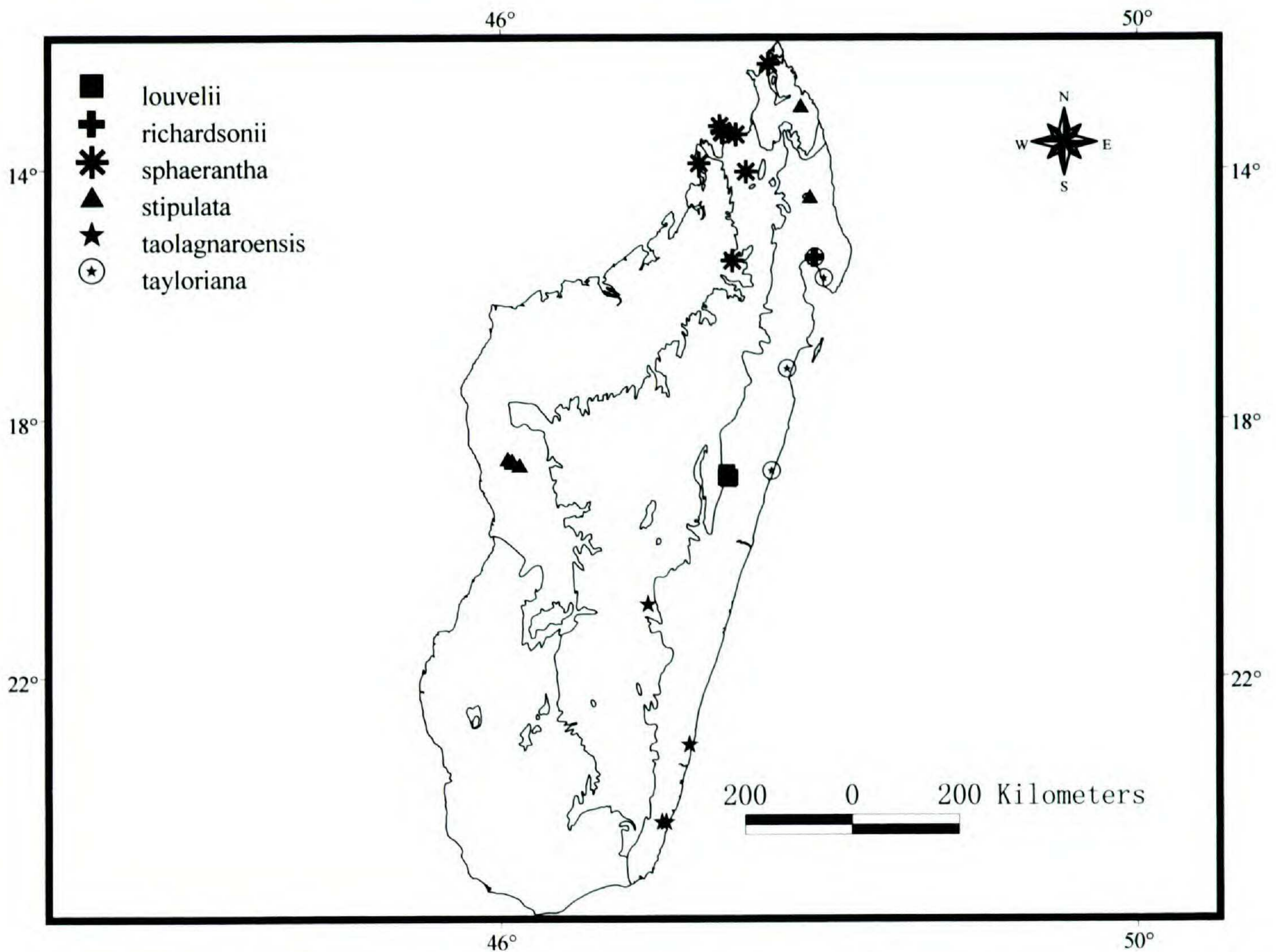


Figure 10. Distribution of *Breonia louvelii*, *B. richardsonii*, *B. sphaerantha*, *B. stipulata*, *B. taolagnaroensis*, and *B. tayloriana*.

Fianarantsoa: District Fort-Carnot, Canton Tolongoina, Ankadilalana, 19295 SF (TEF); Forêt d'Ambatoharanana, 7136 SF (TEF); District Ifanadiana, Ranomafana National Park, *Randrianasolo & Rasabotsy* 32 (MO), 9974 SF (TEF), *Razafimandimbison* SG 389 (MO, TAN). **Mahajanga:** District Befandriana-Nord, Canton Matsondakana, Belalona, Réserve Spéciale d'Anjanaharibe-Sud, *Ravelonarivo & Rabesaonina* 570 (MO). **Toamasina:** District Anosibe an'Ala, Tsaratampona, Mangorobilika, 25526 SF (TEF); District Moramanga, Canton Périnet, Sahamaloto, 6105 SF (TEF).

8. *Breonia louvelii* Homolle, Bull. Soc. Bot. France 84: 461. 1937 [publ. 1938]. TYPE: Madagascar. [Toamasina province], Analama-zotra, Sep. 1925 (fl), *Louvel* 125 (holotype, P!).

Medium-sized trees, 7–10 m tall. Bark with longitudinal fissures. Leafy stems rounded, glabrous, lenticellate. Terminal vegetative buds conical, 5–9 × 1–1.5 mm long, glabrous. Leaves persistent; petioles ca. 7–17 mm long, adaxially canaliculate, glabrous; blades ca. 4–9 × 1.5–3.5 cm, oblanceolate to elliptic, glabrous, coriaceous, glossy, apex acuminate to obtuse, base attenuate; margins glabrous, entire, slightly involute when dry; secondary veins 10 to 11 pairs per side, eucamptodromous, adaxi-

ally inconspicuous, abaxially conspicuous; domatia absent; stipules 5–9 × 1.5–1.8 mm, cymbiform, not carinate, glabrous, free at the base, deciduous. Inflorescence solitary, heads 1.8–2 cm wide; inflorescence axes 2–4 cm long, flattened, slender, glabrous; bracts calyptra-like, deciduous; peduncles ca. 2 mm long, glabrous. Flowers 5-merous or rarely 6-merous; calyx tubes ca. 1 mm long, free, lobes ca. 1 mm long, inside lanate, outside glabrous, lobes densely pubescent, truncate to oblong; corolla tubes 5–6 × 1–1.2 mm, glabrous, lobes 2–3 mm long, broadly oblong; anthers 1–1.5 mm long; filaments 0.2–0.3 mm long; styles 7–8 × 1–1.5 mm; stigmas capitate (shallowly bifid); ovary 2-carpellate; carpels syncarpous; ovule 1 per locule, pendulous; placentae small. Infructescences not seen.

Habitat and distribution. Evergreen rainforests; District of Moramanga (Fig. 10).

Common names. Hazomarotsaka (slender but tall trees), Molompanyady.

Phenology. Flowering September to October; fruiting December to January.

Discussion. This species has a very restricted geographical distribution and appears to be rare.

Additional specimens examined. MADAGASCAR. **Toamasina:** District Moramanga, Canton Périnet, Antaniditra, 7921 SF (TEF); Sahamaloto, 7562 SF (TEF); Réserve Spéciale d'Analamazaotra, *Razafimandimbison* SG 358 (MO, TAN).

9. *Breonia lowryi* Razafim., sp. nov. TYPE: Madagascar. Fianarantsoa province: Ambalavao, Andringitra Reserve, *Lewis et al.* 755 (holotype, MO 05066234; isotypes, K, TAN). Figure 11.

Haec species a congeneris loculis corollinis glabris, tubo calycino intus glabro atque loculis 7- ad 9-ovulatis distinguitur.

Trees, 10–30 m tall. Bark rugose. Leafy stems quadrangular, glabrous. Terminal vegetative buds ca. 3 × 2 mm, glabrous. Leaves persistent, petioles 10–14 mm long, adaxially canaliculate, glabrous; blades (5.5–)7.8–12 × (2.4–)3.4–6.4 cm, obovate, glabrous, coriaceous, not glossy, apex broadly cuspidate, base attenuate; margins glabrous, entire; secondary veins 6 to 9 pairs per side, eucamptodromous, abaxially conspicuous; pit-type domatia in the axils of the secondary veins, pubescent; stipules ca. 5 × 1–1.2 mm, cymbiform, not carinate, glabrous, free at the base, deciduous. Inflorescences solitary, heads 2–2.3 cm wide; inflorescence axes ca. 1.8–3 cm long, flattened, glabrous; bracts calyptra-like, deciduous; peduncles ca. 2 mm long, glabrous. Flowers 5-merous; calyx tubes ca. 2 mm long, inside glabrous, outside puberulent, lobes 0.5–0.8 mm long, oblong, inside glabrous, outside velutinous; corolla tubes ca. 6 × 0.4 mm, reddish, inside puberulous, outside glabrous, lobes 2–2.2 mm long, oblong, puberulous; margins glabrous; anthers 0.5–0.8 mm long; filaments ca. 0.2 mm long, flattened; styles ca. 8 × 0.6 mm; stigmas elongate to capitate; ovary 2-carpellate; carpels syncarpous; ovules 7 to 9 per locule, pendulous; placentae elongated. Infructescence 1.1–1.5 cm diam., with well-developed calyx remnants; individual fruits berry-like; endocarp soft, fibrous; disks accrescent, rounded; seeds 7 to 9 per locule, strongly flattened, with rudimentary wings, red; seed-coat reticulate.

Habitat and distribution. Evergreen forests between 900 and 1500 m altitude; Districts of Fort-Carnot, Moramanga, Ambalavao, and Fianarantsoa (Fig. 12).

Common names. Molompangady, Valompangady.

Phenology. Flowering time unknown; fruiting May and October.

Discussion. This species differs from the other *Breonia* species that also have 7 to 9 ovules per locule and glabrous corolla lobes because the inside of the calyx tubes is glabrous. The epithet of

this new name honors Porter P. Lowry II, head of the Africa and Madagascar Department of the Missouri Botanical Garden, who has done much to further studies of the Araliaceae as well as other plant families in Madagascar.

Paratypes. MADAGASCAR. **Fianarantsoa:** District Fianarantsoa II, Canton Ampamaherana, 2078 SF (TEF); District Fort-Carnot, Canton Tolongoina, Andrambovato, 9711 SF (TEF), 11594 SF (TEF), 14-B-R-230 (TEF). **Toamasina:** District Moramanga, Forêt d'Analamazaotra (Périnet), 24150 SF (TEF).

10. *Breonia macrocarpa* Homolle, Bull. Soc. Bot. Fr. 84: 461. 1937 [publ. 1938]. TYPE: "Madagascar," *Périer de la Bâthie* 3933 (lectotype, designated by Ridsdale (1975: 545), P!). Figures 2D and 3D.

Trees, 10–20 m tall. Bark longitudinally fissured. Leafy stems quadrangular, glabrous. Terminal vegetative buds conical, 27–40 × 4–6 mm, puberulent. Leaves persistent; petioles 35–60 × ca. 4 mm, terete, lenticellate, puberulous; blades 19.5–38 × 15–25 cm, broadly ovate to broadly oblanceolate, brown-tinged when dry, adaxially glabrous, abaxially sericeous, coriaceous, glossy, apex cuspidate to rounded, base rounded; margins glabrous, entire; secondary veins 12 or 13 pairs per side, eucamptodromous, abaxially densely pubescent, adaxially glabrous; tuft-domatia in the axils of secondary and tertiary veins; stipules 27–34 × 6–9.5 mm, cymbiform, abaxially carinate, puberulous, free at the base, deciduous. Inflorescences solitary, heads ca. 4.7 cm wide; inflorescence axes 8.5–12.5 cm, flattened, glabrous to puberulous; bracts calyptra-like, deciduous; peduncles not elongated. Flowers 5-merous or rarely 4-merous; calyx tubes 2.8–3 mm long, green, below the middle velutinous, around the mid-part glabrous, toward the lobes puberulous; lobes ca. 2 mm long, truncate to oblong, velutinous; corolla tubes ca. 11 mm long, glabrous, lobes ca. 3.5 × 0.25 mm long, oblong, glabrous, puberulous toward the apices; margins ciliate; anthers ca. 2 mm long; filaments 0.5–1 mm long, flattened. Styles ca. 21 × 0.5 mm, glabrous; stigmas clavate; ovary 2-carpellate; carpels syncarpous; ovules 4 to 6 per locule, flattened, pendulous, imbricate; placentae strongly flattened, elongated, adnate to the septum. Infructescences 3–4 cm diam., woody when dry, with well-developed calyx remnants; individual fruits with endocarp hard, glossy; disks accrescent, pentagonal; seeds 4 to 6 per locule, strongly flattened, ellipsoid, red, reticulate.

Phenology. Flowering March to May, August to

Additional specimens examined. MADAGASCAR. **Toamasina:** District Moramanga, Canton Périnet, Antaniditra, 7921 SF (TEF); Sahamaloto, 7562 SF (TEF); Réserve Spéciale d'Analamazaotra, *Razafimandimbison* SG 358 (MO, TAN).

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Habitat and distribution. Evergreen forests between 900 and 1500 m altitude; Districts of Fort-Carnot, Moramanga, Ambalavao, and Fianarantsoa (Fig. 12).

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Phenology. Flowering time unknown; fruiting May and October.

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Phenology. Flowering March to May, August to

September; fruiting May to July, December to January.

Habitat and distribution. Low- and mid-altitude of eastern evergreen rainforests; Districts of Brickaville, Moramanga, and Toamasina II (Fig. 5).

Common names. Molompangady and Valotra.

Discussion. Ridsdale (1975: 545) included *Breonia macrocarpa* as a synonym of *B. madagascariensis*, dismissing the former as "a hairy-leaved form" of the latter. However, these two are quite different morphologically, as is clear from Table 3. Despite the striking morphological differences between the two species, *B. macrocarpa* has not been recognized since its original description, partly because Homolle (1938) did not provide keys for the species of *Breonia* she recognized and partly because no collections of *B. madagascariensis* have been made for almost 200 years.

While describing this species, Homolle cited three specimens, *Thouvenot 117* (P!), *Perrier de Bâthie 3933* (P!), and *Perrier de la Bâthie 5270* (P!), without selecting the type species.

Additional specimens examined. MADAGASCAR. **Toamasina:** District Brickaville, Fetromby, Ambalakoandro, 3265 SF (TEF); District Moramanga, Perinét, 26906 SF (TAN), *Noyes et al. 974* (K, MO, P, TAN), *Razafiman-dimbison SG 352* (MO, P, TAN); District Toamasina II, Canton Ambodiriana, Vohimarangitra, 9052 RN (P), 9129 RN (P); Canton Ambodiriana, 18116 SF (P, TEF), 21160 SF (TEF), 28136 SF (TEF), 32344 SF (TEF).

11. *Breonia madagascariensis* A. Rich., in DC., Prodr. 4: 620. Sep. 1830. *Sarcocephalus madagascariensis* (A. Rich.) Baill., Adansonia 12: 311. 1879. TYPE: "Madagascar." [Without exact locality], *Chapelier s.n.* (lectotype, designated by Ridsdale (1975: 545), K!; isolecotype, P!). Figure 1F.

Trees, height unknown. Bark rugose. Leafy stems quadrangular, glabrous. Terminal vegetative buds conical, ca. 35 × 6 mm, glabrous. Leaves persistent, subsessile; blades ca. 45 × 35 cm, broadly obovate to broadly spatulate, glabrous, coriaceous, not glossy, apex caudate, base attenuate; midrib angular, lenticellate, prominent; margins glabrous, entire; secondary veins 18 or 19 pairs per side, eucamp-todromous, abaxially prominent; domatia absent; stipules ca. 35 mm long, cymbiform, abaxially car-

inate, glabrous, free at the base, deciduous. Inflorescences solitary, heads ca. 6 cm wide; inflorescence axes 16–21 cm long, flattened, puberulous; bracts calyptra-like, deciduous; peduncles not elongated. Flowers 5-merous; calyx tubes ca. 3 mm long, with prominulous ribs, inside lanate, outside glabrous except on upper parts of ribs, lobes ca. 2 mm long, oblong to truncate, pubescent; corolla tubes ca. 14 × 1.5 mm, ribbed, glabrous, lobes ca. 3 × 1 mm, oblong, inside glabrous, outside puberulous in upper third, margins ciliate; anthers ca. 2 mm long; filaments 0.25–0.5 mm long, flattened; styles 17–18 × ca. 0.25 mm, glabrous; stigmas clavate; ovary 2-carpellate; carpels syncarpous; ovules 8 per locule, pendulous, imbricate; placentae strongly flattened, elongated. Infructescences not seen.

Habitat and distribution. Habitat unknown; Madagascar.

Phenology. Unknown.

Discussion. *Breonia madagascariensis* is known only from the six authentic herbarium specimens collected by Commerson, Chapelier, and Bréon during the early botanical explorations they undertook separately in 1770–1771, 1794–1808, and 5 September–5 December 1818, respectively (Dorr, 1997). No collecting localities were mentioned on their labels. This species has not been collected since 1818.

Chapelier is known to have resided on the East Coast at Foulpointe for a dozen years, and he established an experimental garden in a place known locally as Isatrano (Tamatave or Toamasina). Also, he made botanical collections around Ivoloina, Foulpointe, and on the island of St. Marie (all within Toamasina province). Hence, it is possible that *Breonia madagascariensis* was collected from the above-mentioned areas of the east coast of Madagascar. Most of the eastern coast of the country has been deforested for agricultural purposes and replaced by secondary vegetation characterized by the dominance of *Ravenala madagascariensis* Sonn. (Strelitziaceae). However, *B. madagascariensis* may still be extant inside protected forests (Betampona Reserve, Zahamena Reserve, Analamazaotra Reserve) in this area, so efforts to rediscover *B. madagascariensis* should focus on these three protected areas and their surroundings.

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Figure 11. *Breonia lowryi*.—A. Fertile branch with young infructescence. —B. Mature infructescence. —C. Seed, showing flattened lateral profile (left); dorsal view (right). —D. Median dissection through fruit, showing calyx tube and bicarpellate ovary with 7 to 9 pendulous ovules per locule (left); entire fruit (right). —E. Two adjacent flowers, showing two adjacent ovaries separated: median dissection through flower, showing glabrous corolla and pubescent calyx tubes and bicarpellate ovary with ovules (left); entire flower, showing only part of corolla tube (right). *Lewis et al. 755* (MO).

September; fruiting May to July, December to January.

Habitat and distribution. Low- and mid-altitude of eastern evergreen rainforests; Districts of Brickaville, Moramanga, and Toamasina II (Fig. 5).

Common names. Molompangady and Valotra.

Discussion. Ridsdale (1975: 545) included *Breonia macrocarpa* as a synonym of *B. madagascariensis*, dismissing the former as "a hairy-leaved form" of the latter. However, these two are quite different morphologically, as is clear from Table 3. Despite the striking morphological differences between the two species, *B. macrocarpa* has not been recognized since its original description, partly because Homolle (1938) did not provide keys for the species of *Breonia* she recognized and partly because no collections of *B. madagascariensis* have been made for almost 200 years.

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Additional specimens examined. MADAGASCAR. **Toamasina:** District Brickaville, Fetromby, Ambalakoandro, 3265 SF (TEF); District Moramanga, Perinét, 26906 SF (TAN), *Noyes et al. 974* (K, MO, P, TAN), *Razafiman-dimbison SG 352* (MO, P, TAN); District Toamasina II, Canton Ambodiriana, Vohimarangitra, 9052 RN (P), 9129 RN (P); Canton Ambodiriana, 18116 SF (P, TEF), 21160 SF (TEF), 28136 SF (TEF), 32344 SF (TEF).

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Trees, height unknown. Bark rugose. Leafy stems quadrangular, glabrous. Terminal vegetative buds conical, ca. 35 × 6 mm, glabrous. Leaves persistent, subsessile; blades ca. 45 × 35 cm, broadly obovate to broadly spatulate, glabrous, coriaceous, not glossy, apex caudate, base attenuate; midrib angular, lenticellate, prominent; margins glabrous, entire; secondary veins 18 or 19 pairs per side, eucamp-todromous, abaxially prominent; domatia absent; stipules ca. 35 mm long, cymbiform, abaxially car-

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Habitat and distribution. Habitat unknown; Madagascar.

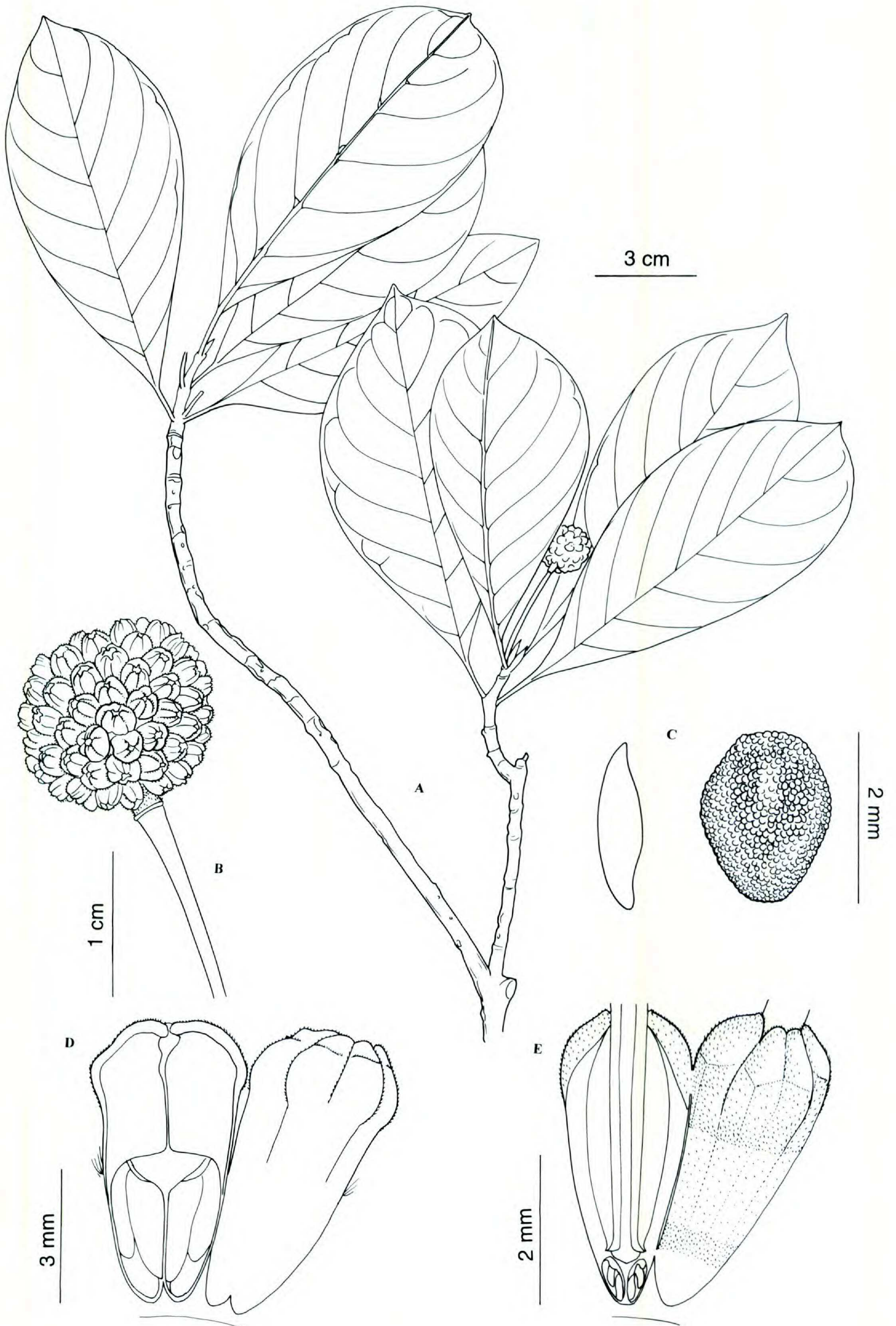
Phenology. Unknown.

Discussion. *Breonia madagascariensis* is known only from the six authentic herbarium specimens collected by Commerson, Chapelier, and Bréon during the early botanical explorations they undertook separately in 1770–1771, 1794–1808, and 5 September–5 December 1818, respectively (Dorr, 1997). No collecting localities were mentioned on their labels. This species has not been collected since 1818.

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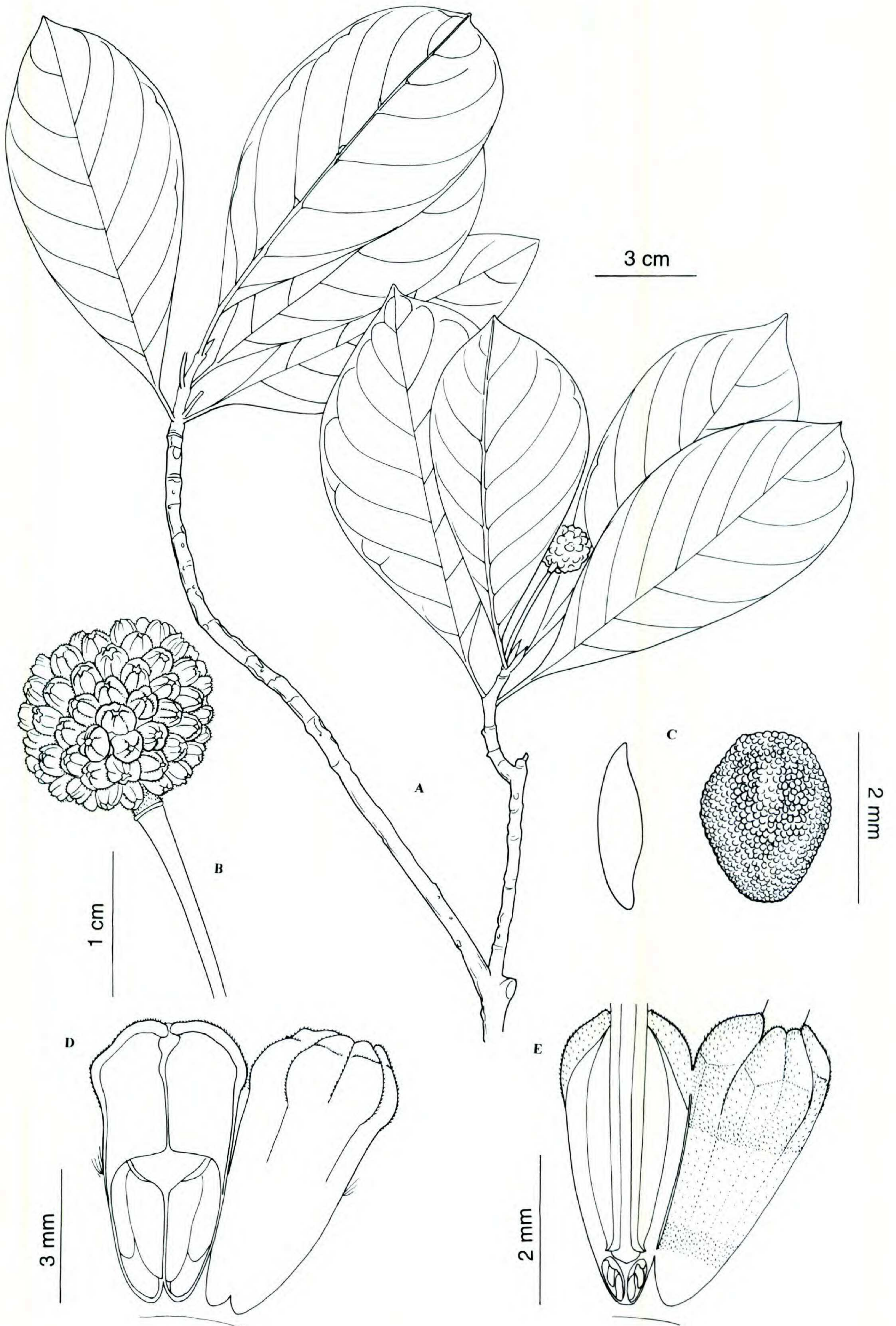


Table 3. Distinctive vegetative morphological features separating *Breonia macrocarpa* and *B. madagascariensis*.

Characters	<i>Breonia macrocarpa</i>	<i>B. madagascariensis</i>
Petioles	well developed	subsessile
Leaf blade size	19–38 × 15–25 cm	45 × 35 cm
Abaxial indumentum on leaf blades	densely pubescent	glabrous
Midrib shape	rounded	angular
Domatia	present	absent
Peduncle length	8.5–12.5 cm	16–21 cm

The lectotype *Chapelier s.n.* selected by Ridsdale (1975) was from the six known collections.

Additional specimens examined. “Madagascar, Herbar E. Drake, P-0013910 (P); “Madagascar, herbarium Richard, P-00132909 (P),” *Bréon s.n.* (P), *Commerson s.n.* (P not seen).

12. *Breonia membranacea* Havil., J. Linn. Soc. Bot. 33: 36. 1897. TYPE: “Madagascar.” [Without exact locality], *Perrottet s.n.* (lectotype, designated by Ridsdale (1975: 545), P!).

Trees, 12–18 m tall. Bark rugose. Leafy stems terete, glabrous. Terminal vegetative buds conical, 10–20 × ca. 1.5 mm, puberulent at the base. Leaves persistent; petioles 3–6 mm long, adaxially canaliculate, puberulous when young, glabrescent; blades 8.5–12.2 × 4.5–5.4 cm, oblong, glabrous, membranaceous, adaxially glossy, apex broadly cuspidate to acute, base rounded; margins glabrous, entire; secondary veins ca. 8 pairs per side, eucamptodromous, adaxially prominulous; domatia hairy in the axils of the secondary veins; stipules 12–21 mm long, cymbiform, not carinate, glabrous, free at the base, deciduous. Inflorescences solitary, heads ca. 2.2 cm wide; inflorescence axes 4.5–5.5 cm long, strongly flattened, glabrous; bracts calyptra-like, deciduous; peduncles ca. 3 mm long, glabrous. Flowers 5-merous; calyx tubes 1–1.2 mm long, inside lanate, outside glabrous, lobes 0.5–0.7 mm long, oblong, velutinous; corolla tubes ca. 5 × 0.5–0.7 mm, inside puberulous, outside glabrous, lobes ca. 2 mm long, obtuse to truncate, puberulous, margins ciliate; anthers ca. 1 mm long; filaments ca. 2 mm long, flattened, glabrous; styles 7–8 × ca. 0.5 mm, glabrous; stigmas capitate; ovary 2-carpellate; carpels syncarpous; ovules 3 per locule, flattened, pendulous, imbricate; placentae small, elongated. Infructescences 1.5–1.8 cm diam., with well-developed calyx remnants; individual fruits with endocarp soft, fibrous; disks accrescent, heart-shaped; seeds 1 to 3 per locule, flattened, concavo-convex, ellipsoid, red; seed-coat reticulate.

Habitat and distribution. Evergreen lowland rainforests, littoral forests; Districts of Moramanga and Fénériver Est (Fig. 12).

Common names. Molompangady, Valotra.

Phenology. Flowering January to February; fruiting March to April.

Discussion. This species is distinct in its leaves with relatively short petioles. The lectotypification made by Ridsdale is questionable because the lectotype, *Perrottet s.n.*, does not match with Haviland's (1897) remarks concerning the terminal vegetative buds of *B. membranacea*: “I have seen none [specimens] with the apex uninjured.” *Perrottet s.n.* has an intact and uninjured apex and was annotated by Haviland as *Breonia membranacea*. Haviland clearly stated that the type specimen of *B. membranacea* was in the Paris herbarium. Haviland mentioned that the description of *Breonia mauritiana* was based on a single specimen; he did not mention that this was also the case for *B. membranacea*. Hence, he could possibly have seen more than one specimen of *B. membranacea*, although he did not cite any other specimens in the original description.

Haviland is known to have visited the herbaria at the British Museum (BM), Leiden (L), and Paris (P) (Haviland, 1897). However, from Kew (K), L, and P, I received only the specimen of *Perrottet s.n.* from P. It is possible that the “injured” specimens seen by Haviland are at BM. Ridsdale visited all three herbaria while preparing his revision of African and Madagascar Naucleae (Ridsdale, 1975); he did not cite any syntype for *B. membranacea*. This implies that he saw only the specimen of *Perrottet s.n.* at Paris. Before one can attempt to resolve the nomenclatural problem of *B. membranacea*, one must visit BM, L, and P and look for possible specimens of *B. membranacea* annotated by Haviland.

Additional specimens examined. MADAGASCAR. **Toamasina:** District Fénériver-Est, Ampasina, Tampolo, 13094 SF (TEF), 16496 SF (TEF), 16621 SF (P); District Moramanga, Forêt d'Analamazaotra, *Louvel 186* (P).

13. *Breonia perrieri* Homolle, Bull. Soc. Bot. Fr. 84: 461. 1937 [publ. 1938]. TYPE: Madagascar. [Toliara province]; Morondava, Forêt de Marofandilia, *Perrier de la Bâthie 3513* (lectotype, designated by Ridsdale (1975: 546), P!).

Medium-sized trees, ca. 8 to 15 m tall. Bark with longitudinal fissures. Leafy stems flattened, lenticellate, glabrous. Terminal vegetative buds conical, 9–11 × 3–4 mm, glabrous. Leaves deciduous; petioles 33–60 × 1.5–1.8 mm, terete, glabrous or pubescent toward the apex, lenticellate; blades 9–15 × 6–13

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Habitat and distribution. Evergreen lowland rainforests, littoral forests; Districts of Moramanga and Fénérive Est (Fig. 12).

Common names. Molompangady, Valotra.

Phenology. Flowering January to February; fruiting March to April.

Discussion. This species is distinct in its leaves with relatively short petioles. The lectotypification made by Ridsdale is questionable because the lectotype, *Perrottet s.n.*, does not match with Haviland's (1897) remarks concerning the terminal vegetative buds of *B. membranacea*: “I have seen none [specimens] with the apex uninjured.” *Perrottet s.n.* has an intact and uninjured apex and was annotated by Haviland as *Breonia membranacea*. Haviland clearly stated that the type specimen of *B. membranacea* was in the Paris herbarium. Haviland mentioned that the description of *Breonia mauritiana* was based on a single specimen; he did not mention that this was also the case for *B. membranacea*. Hence, he could possibly have seen more than one specimen of *B. membranacea*, although he did not cite any other specimens in the original description.

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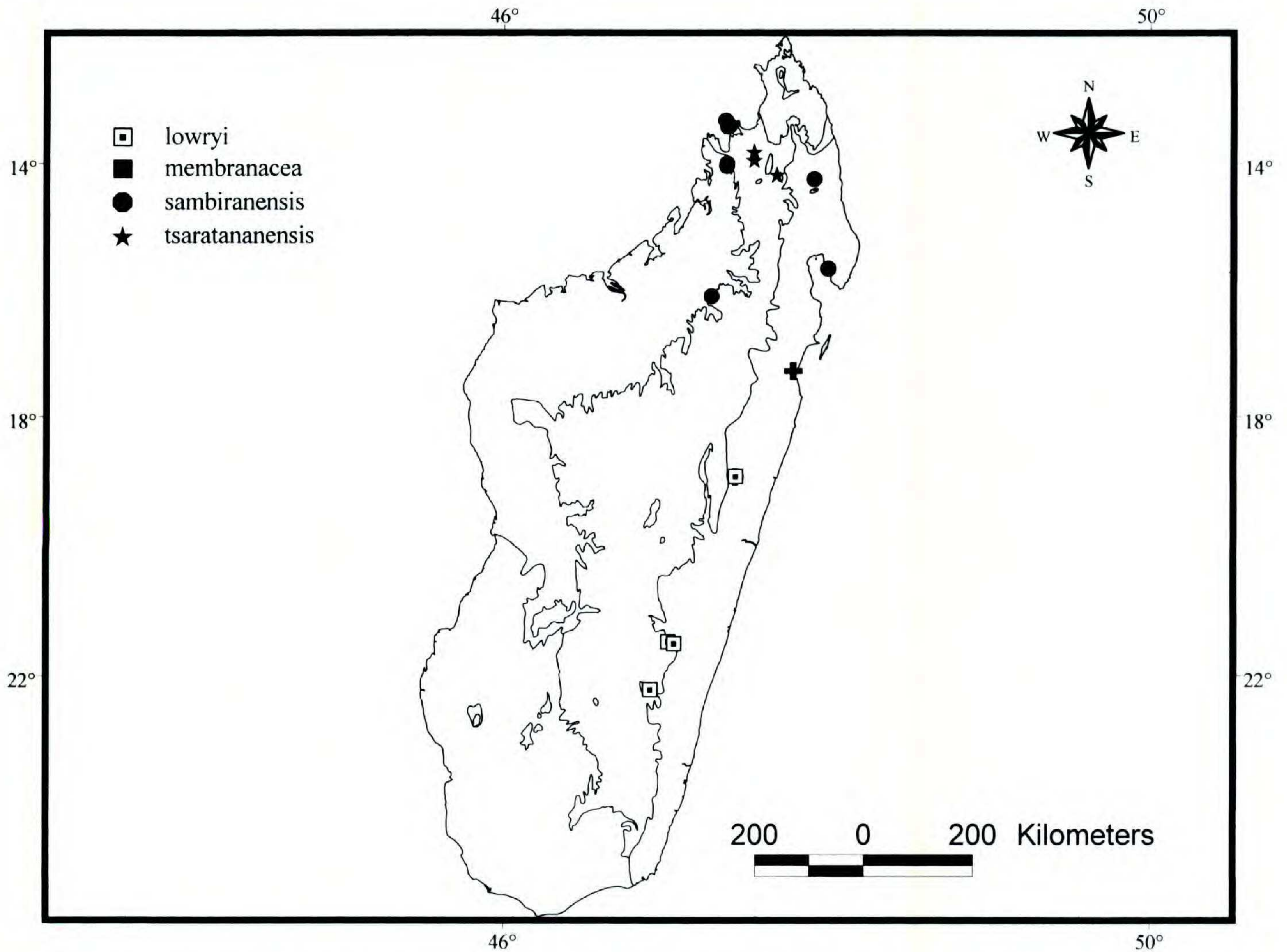


Figure 12. Distribution of *Breonia lowryi*, *B. membranacea*, *B. sambiranensis*, and *B. tsaratananensis*.

cm, broadly obovate to orbicular, pubescent or glabrous, coriaceous or rarely membranaceous, apex cuspidate to rounded, base cordate; margins glabrous, entire; secondary veins ca. 9 pairs per side, the first 3 diverging from the base of the midrib, prominulous; domatia absent; stipules 8–14 × 3–4.2 mm, cymbiform, abaxially carinate, glabrous, free at the base, deciduous. Inflorescences solitary, heads 2.5–2.9 cm wide; inflorescence axes 2.4–3.5 cm long, terete, pubescent or glabrous; bracts calyptra-like, deciduous; peduncles 2–3 mm long. Flowers 5-merous; calyx tubes ca. 2.5 mm long, green, inside below the middle glabrous, velutinous from the middle toward the base of lobes, outside glabrous, lobes 1–1.2 mm long, oblong, puberulous; corolla tubes 4–5 × ca. 1 mm, yellow-tinged, glabrous, lobes ca. 1.5 mm long, oblong, glabrous; anthers 1–1.1 mm long; filaments ca. 1 mm long, flattened, glabrous; styles ca. 10 × 0.2 mm, glabrous; stigmas globose to clavate; ovary 2-carpellate; carpels syncarpous; ovules 2 to 3 per locule, strongly flattened, pendulous, imbricate; placentae small, elongated. Infructescences 1.8–2.2 cm diam., with well-developed calyx remnants; individual fruits with endocarp hard, glossy; disks accrescent, heart-shaped; seeds 1 to 2 per loc-

ule, with rudimentary wings at the base, strongly flattened, ellipsoid, white-tinged; seed-coat reticulate.

Phenology. Flowering November to January; fruiting January to March.

Habitat and distribution. Western and northwestern deciduous dry forests; from Districts of Antsiranana II and Ambato-Boeni, Befandriana-Nord, Soalala, Antsalova, Belo Tsiribihina, Maintirano, Marovoay, Ambilobe, and Vohémar (Fig. 5).

Common name. Valotra.

Phenology. Flowering November–December; fruiting January–February.

Discussion. The following were among the four specimens cited by Homolle in the protologue of *Breonia perrieri*: *Perrier de la Bâthie* 825 (P not seen), *Perrier de la Bâthie* 17852 (P not seen), and *Greve s.n.* (P not seen).

Additional specimens examined. MADAGASCAR. **Antsiranana:** District Antsiranana II, Ankarana, Ambilomangodro, Forêt de Bezono, 29653 *SF* (TEF); Mahamasina, Réserve Spéciale d'Ankarana, *Malcomber et al.* 1833 (K, MO, P, TAN), *Razafimandimbison* SG 273 (MO, P, TAN); Forêt d'Ambre, 6181 *SF* (TEF), 6616 *SF* (TEF); Plateau d'Ankarana à l'ouest d'Ambondromifehy, 3026 *SF* (K, TEF); District Vohémar, Forêt d'Analafiana au nord de la base

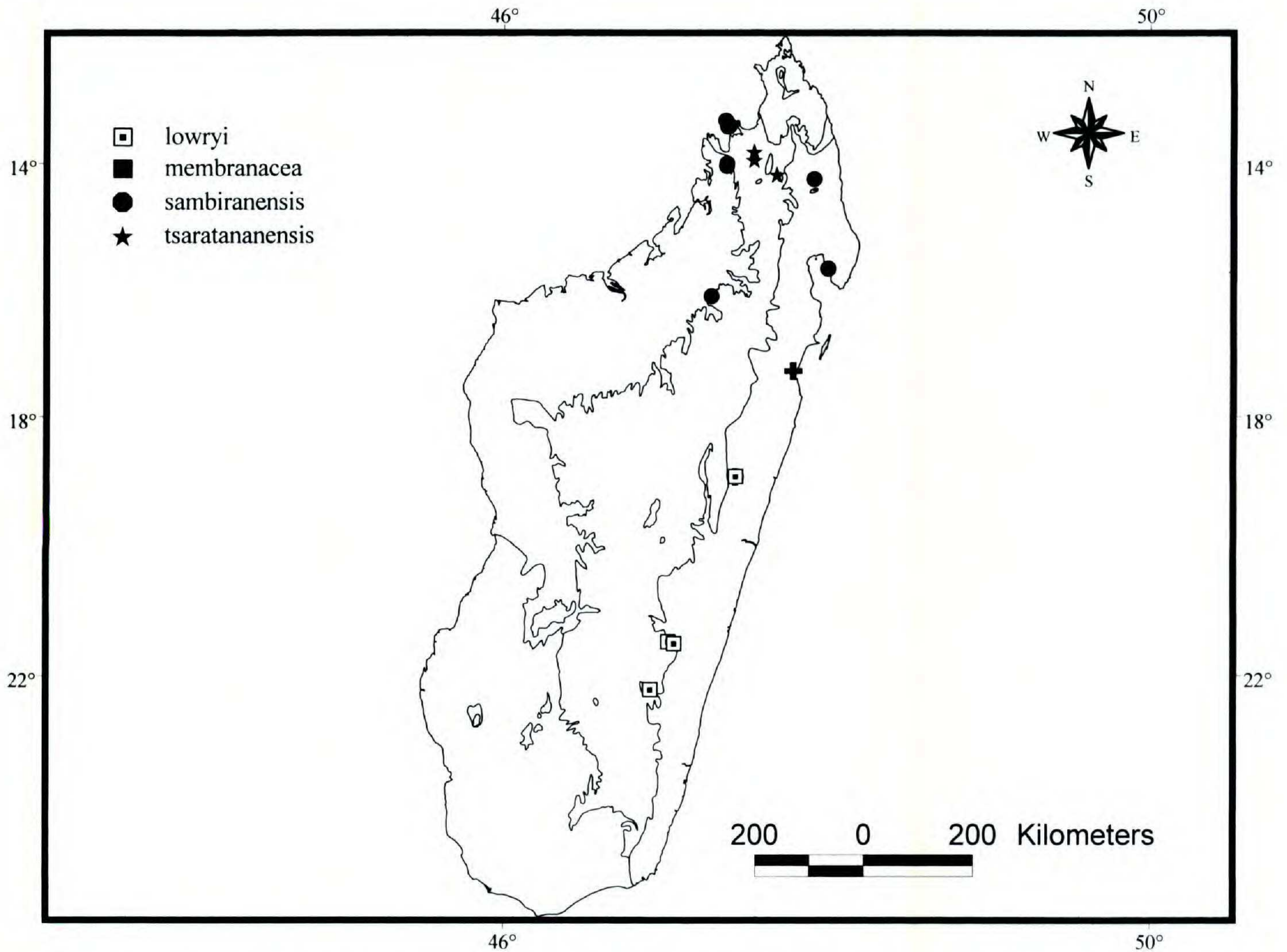


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ule, with rudimentary wings at the base, strongly flattened, ellipsoid, white-tinged; seed-coat reticulate.

Phenology. Flowering November to January; fruiting January to March.

Habitat and distribution. Western and northwestern deciduous dry forests; from Districts of Antsiranana II and Ambato-Boeni, Befandriana-Nord, Soalala, Antsalova, Belo Tsiribihina, Maintirano, Marovoay, Ambilobe, and Vohémar (Fig. 5).

Common name. Valotra.

Phenology. Flowering November–December; fruiting January–February.

Discussion. The following were among the four specimens cited by Homolle in the protologue of *Breonia perrieri*: *Perrier de la Bâthie* 825 (P not seen), *Perrier de la Bâthie* 17852 (P not seen), and *Greve s.n.* (P not seen).

Additional specimens examined. MADAGASCAR. **Antsiranana:** District Antsiranana II, Ankarana, Ambiloman-godro, Forêt de Bezono, 29653 *SF* (TEF); Mahamasina, Réserve Spéciale d'Ankarana, *Malcomber et al.* 1833 (K, MO, P, TAN), *Razafimandimbison* SG 273 (MO, P, TAN); Forêt d'Ambre, 6181 *SF* (TEF), 6616 *SF* (TEF); Plateau d'Ankarana à l'ouest d'Ambondromifehy, 3026 *SF* (K, TEF); District Vohémar, Forêt d'Analafiana au nord de la base

Manambery, 27503 *SF* (TEF); 14 km E of Vohémar, near Analafiana, 15673 *SF* (TEF); Ankara, 6696 *SF* (TEF). **Mahajanga:** District Ambato-Boeni, Ankirihitra, Forêt d'Anatiale, 19379 *SF* (TEF); District Befandriana-Nord, Ambahivahy, Forêt d'Andembikely, 19061 *SF* (TEF); Forêt de Marohogo à l'ouest de Mahajanga, 18450 *SF* (TEF); District Antsalova, à 3 km à l'Est de Bevitika, *Labat & Conté* 2674 (K, MO, P, TAN), *Labat et al.* 2261 (K, MO, P, TAN); Plateau de Bemaraha, aux environs de Tsiandro, 6754 *SF* (TEF), *Jongkind et al.* 3412 (K, MO, P, TAN), *Villiers et al.* 4846 (MO, P, TAN); District Soalala, Commune Andranomavo, 3882 *SF* (TAN), Andranomavo, 17565 *SF* (TEF). **To-liara:** District Belo Tsiribihina, Tsimafana, Ankirijifotsy, 7987 *SF* (TEF), *Noyes et al.* 1028 (K, MO, P, TAN); District Morondava, Tsimembo-limite concession de M. Barthe, 8245 *SF* (TEF); Ankilatsy, 4677 *SF* (TEF).

14. *Breonia richardsonii* Razafim., sp. nov.
TYPE: Madagascar. [Toamasina province]: Maroantsetra, Jardin botanique de Farankaraina, 16 June 1965 (fl), 14359 *SF* (holotype, TEF). Figure 13.

Haec species a congeneris inflorescentiae bracteis tubulosis adpressis in 1 triangulares tres quatuorve desinentibus atque ovariis contiguis post anthesin distinguitur.

Trees, 15–30 m tall. Bark fissured longitudinally. Leafy stems terete, glabrous. Terminal vegetative buds conical, 3–4 × 1–1.5 mm, glabrous. Leaves persistent; petioles 7–10 × ca. 1 mm, terete, glabrous; blades 5–7.7 × 2.5–3.7 cm, oblanceolate to ovate, glabrous, membranaceous, apex cuspidate to acute, base acute; margins glabrous, entire; secondary veins 5 to 7 pairs per side, eucamptodromous, inconspicuous; domatia cryptic-type in the secondary veins, glabrous, adaxially prominent; stipules ca. 5 × 1–1.5 mm, cymbiform, not carinate, free at the base, deciduous. Inflorescence solitary, heads ca. 2 cm wide; inflorescence axes 2.5–3 cm long, terete, glabrous; peduncles ca. 5 mm long; bracts tubular with 3–4 broadly triangular lobes, not enclosing the young inflorescence, persistent. Flowers 5-merous or rarely 4-merous; calyx tubes ca. 1 mm long, inside glabrous, except at the base velutinous, outside at the base velutinous, in the mid-parts glabrous, toward the lobes puberulous, lobes broadly triangular, puberulous; corolla tubes ca. 4 × 0.3–0.5 mm, glabrous, lobes ca. 1.5 mm long, oblong, glabrous; anthers 2–2.5 mm long; filaments ca. 0.1 mm long, flattened; styles ca. 7 × 0.5 mm, glabrous; stigmas globose to clavate; ovary 2-carpellate, adjacent ovaries fused only at the base; carpels syncarpous; ovules 5 per locule, pendulous, imbricate; placentae large, elongated, occupying the upper third of the locule. Infructescences 1–1.5 cm diam., with well-developed calyx remnants, adjacent ovaries fused up to the mid-point; individual fruits with endocarp soft, fibrous; disks accrescent, obconical; seeds 5 per loc-

ule, strongly flattened, ellipsoid, angular, red; seed-coat reticulate.

Habitat and distribution. Lowland rainforests; District of Maroantsetra (Fig. 10).

Common names. Valotrafotsy.

Phenology. Flowering April; fruiting November.

Discussion. This species is very different from other species of *Breonia* because of its tubular, appressed inflorescence bracts with 3 to 4 broadly triangular lobes and post-anthesis fusion of adjacent ovaries. The specific epithet honors Mick Richardson, who was my Ph.D. advisor as well as the Manager of the Graduate Program at the Missouri Botanical Garden. This species is extremely rare and has not been collected since 1965.

Paratype. MADAGASCAR. **Toamasina:** District Maroantsetra, Jardin botanique de Farankaraina, 18311 *SF* (TEF).

15. *Breonia sambiranensis* Razafim., sp. nov.
TYPE: Madagascar. [Antsiranana province]: Nosy be, Réserve Naturelle Intégrale de Lokobe, 13°24'S, 48°20'E, 350 m, 7 July 1995 (fl), *Antilahimena* 237 (holotype, TAN; isotype, MO). Figures 3C, 4D, and 14.

Haec species a congeneris calycis tubo brevi prominule costato et lobulis brevibus in centro non profunde foveolatis, ad margines protuberationes breves stylum versus directas gerentibus distinguitur.

Trees, rarely shrubs, (6–)10–20 m tall. Bark smooth, glabrous. Leafy stems quadrangular, glabrous, lenticellate. Terminal vegetative buds conical, ca. 5 × 2–3 mm, glabrous. Leaves persistent; petioles 15–30 mm long, adaxially canaliculate, glabrous; blades (8.5–)12–17.5 × 4.7–9.5 cm, broadly ovate to broadly obovate, or broadly ovate to narrowly ovate, glabrous, coriaceous, glossy, apex mucronulate to acute or mucronulate to obtuse, base cuneate, lower surfaces yellow-red-tinged when dry; margins entire, glabrous; secondary veins 5 to 9 per side, eucamptodromous, dark red when dry, abaxially prominulous; domatia absent; stipules 6–7 × 4–5 mm, cymbiform, not carinate, glabrous, free at the base, deciduous. Inflorescence solitary, heads 3–3.7 cm wide; inflorescence axes 2.5–3 cm long, flattened, glabrous; bracts calyptra-like, deciduous; peduncles 1.5–2.2 mm long, glabrous. Flowers 5-merous; calyx tubes 1–1.2 mm long, infundibular, prominulously ribbed, glabrous; lobes 0.2–0.3 mm long, truncate, bearing a shallow depression in the center, a short protuberance on the edge toward the style (Fig. 14D), tomentose; corolla tubes 7–8 × 0.8–0.9 mm, inside puberulous, outside glabrous, lobes ca. 3 mm long, oblong,

Manambery, 27503 *SF* (TEF); 14 km E of Vohémar, near Analafiana, 15673 *SF* (TEF); Ankara, 6696 *SF* (TEF). **Mahajanga:** District Ambato-Boeni, Ankirihitra, Forêt d'Anatiale, 19379 *SF* (TEF); District Befandriana-Nord, Ambahivahy, Forêt d'Andembikely, 19061 *SF* (TEF); Forêt de Marohogo à l'ouest de Mahajanga, 18450 *SF* (TEF); District Antsalova, à 3 km à l'Est de Bevitika, *Labat & Conté* 2674 (K, MO, P, TAN), *Labat et al.* 2261 (K, MO, P, TAN); Plateau de Bemaraha, aux environs de Tsiandro, 6754 *SF* (TEF), *Jongkind et al.* 3412 (K, MO, P, TAN), *Villiers et al.* 4846 (MO, P, TAN); District Soalala, Commune Andranomavo, 3882 *SF* (TAN), Andranomavo, 17565 *SF* (TEF). **To-liara:** District Belo Tsiribihina, Tsimafana, Ankirijifotsy, 7987 *SF* (TEF), *Noyes et al.* 1028 (K, MO, P, TAN); District Morondava, Tsimembo-limite concession de M. Barthe, 8245 *SF* (TEF); Ankilatsy, 4677 *SF* (TEF).

14. *Breonia richardsonii* Razafim., sp. nov.
TYPE: Madagascar. [Toamasina province]: Maroantsetra, Jardin botanique de Farankaraina, 16 June 1965 (fl), 14359 *SF* (holotype, TEF). Figure 13.

Haec species a congeneris inflorescentiae bracteis tubulosis adpressis in 1 triangulares tres quatuorve desinentibus atque ovariis contiguis post anthesin distinguitur.

Trees, 15–30 m tall. Bark fissured longitudinally. Leafy stems terete, glabrous. Terminal vegetative buds conical, 3–4 × 1–1.5 mm, glabrous. Leaves persistent; petioles 7–10 × ca. 1 mm, terete, glabrous; blades 5–7.7 × 2.5–3.7 cm, oblanceolate to ovate, glabrous, membranaceous, apex cuspidate to acute, base acute; margins glabrous, entire; secondary veins 5 to 7 pairs per side, eucamptodromous, inconspicuous; domatia cryptic-type in the secondary veins, glabrous, adaxially prominent; stipules ca. 5 × 1–1.5 mm, cymbiform, not carinate, free at the base, deciduous. Inflorescence solitary, heads ca. 2 cm wide; inflorescence axes 2.5–3 cm long, terete, glabrous; peduncles ca. 5 mm long; bracts tubular with 3–4 broadly triangular lobes, not enclosing the young inflorescence, persistent. Flowers 5-merous or rarely 4-merous; calyx tubes ca. 1 mm long, inside glabrous, except at the base velutinous, outside at the base velutinous, in the mid-parts glabrous, toward the lobes puberulous, lobes broadly triangular, puberulous; corolla tubes ca. 4 × 0.3–0.5 mm, glabrous, lobes ca. 1.5 mm long, oblong, glabrous; anthers 2–2.5 mm long; filaments ca. 0.1 mm long, flattened; styles ca. 7 × 0.5 mm, glabrous; stigmas globose to clavate; ovary 2-carpellate, adjacent ovaries fused only at the base; carpels syncarpous; ovules 5 per locule, pendulous, imbricate; placentae large, elongated, occupying the upper third of the locule. Infructescences 1–1.5 cm diam., with well-developed calyx remnants, adjacent ovaries fused up to the mid-point; individual fruits with endocarp soft, fibrous; disks accrescent, obconical; seeds 5 per loc-

ule, strongly flattened, ellipsoid, angular, red; seed-coat reticulate.

Habitat and distribution. Lowland rainforests; District of Maroantsetra (Fig. 10).

Common names. Valotrafotsy.

Phenology. Flowering April; fruiting November.

Discussion. This species is very different from other species of *Breonia* because of its tubular, appressed inflorescence bracts with 3 to 4 broadly triangular lobes and post-anthesis fusion of adjacent ovaries. The specific epithet honors Mick Richardson, who was my Ph.D. advisor as well as the Manager of the Graduate Program at the Missouri Botanical Garden. This species is extremely rare and has not been collected since 1965.

Paratype. MADAGASCAR. **Toamasina:** District Maroantsetra, Jardin botanique de Farankaraina, 18311 *SF* (TEF).

15. *Breonia sambiranensis* Razafim., sp. nov.
TYPE: Madagascar. [Antsiranana province]: Nosy be, Réserve Naturelle Intégrale de Lokobe, 13°24'S, 48°20'E, 350 m, 7 July 1995 (fl), *Antilahimena* 237 (holotype, TAN; isotype, MO). Figures 3C, 4D, and 14.

Haec species a congeneris calycis tubo brevi prominule costato et lobulis brevibus in centro non profunde foveolatis, ad margines protuberationes breves stylum versus directas gerentibus distinguitur.

Trees, rarely shrubs, (6–)10–20 m tall. Bark smooth, glabrous. Leafy stems quadrangular, glabrous, lenticellate. Terminal vegetative buds conical, ca. 5 × 2–3 mm, glabrous. Leaves persistent; petioles 15–30 mm long, adaxially canaliculate, glabrous; blades (8.5–)12–17.5 × 4.7–9.5 cm, broadly ovate to broadly obovate, or broadly ovate to narrowly ovate, glabrous, coriaceous, glossy, apex mucronulate to acute or mucronulate to obtuse, base cuneate, lower surfaces yellow-red-tinged when dry; margins entire, glabrous; secondary veins 5 to 9 per side, eucamptodromous, dark red when dry, abaxially prominulous; domatia absent; stipules 6–7 × 4–5 mm, cymbiform, not carinate, glabrous, free at the base, deciduous. Inflorescence solitary, heads 3–3.7 cm wide; inflorescence axes 2.5–3 cm long, flattened, glabrous; bracts calyptra-like, deciduous; peduncles 1.5–2.2 mm long, glabrous. Flowers 5-merous; calyx tubes 1–1.2 mm long, infundibular, prominulously ribbed, glabrous; lobes 0.2–0.3 mm long, truncate, bearing a shallow depression in the center, a short protuberance on the edge toward the style (Fig. 14D), tomentose; corolla tubes 7–8 × 0.8–0.9 mm, inside puberulous, outside glabrous, lobes ca. 3 mm long, oblong,

recurved, with protuberance abaxially (Fig. 14E), glabrous, with a few scattered hairs at the apex, ciliate; anthers ca. 1.2 mm long; filaments 0.1–0.2 mm long; styles ca. 13×0.1 mm; stigmas clavate; ovary 2-carpellate; carpels syncarpous; ovules 4 to 5 per locule, flattened, imbricate; placentae elongated, strongly flattened. Infructescences 1.2–1.6 cm diam., with accrescent calyx remnants; individual fruits with endocarps soft, fibrous; disks accrescent, napiform; seeds 4 to 5 per locule, concavo-convex, ellipsoid, red; seed-coat reticulate.

Habitat and distribution. This species occurs in low- and mid-altitude evergreen rainforests; Districts of Nosy Be, Ambanja, and Maroantsetra (Fig. 12).

Common name. Valotra.

Phenology. Flowering March to July; fruiting October to November.

Discussion. This species is distinct in its short calyx tubes prominently ribbed, short calyx lobes with shallow depressions in the center, and short protuberances on the edge toward the style (Fig. 14D). The specific epithet refers to the Sambirano regions.

Paratypes. MADAGASCAR. **Antananarivo:** District Ankazobe, Forêt d'Ambositantely, 8413 SF (TEF). **Antsiranana:** District Ambanja, Manongarivo Special Reserve, Massif de Bekolosy, 11430 SF (TEF); District Nosy be, Lokobe, 9220 SF (TEF), 11407 SF (TEF), 24753 SF (TEF), 5524 RN (TEF), *Birkinshaw* 59 (K, MO); Bemarivo, Androranga, ravin de Betsomanga, 841 SF (K, MO, TEF). **Toamasina:** District Maroantsetra, Masoala Peninsula, S of the village of Ambanizana, *Behasy & Vasey* 203 (MO), *Rabe* 115 (MO).

16. *Breonia sphaerantha* (Baill.) Homolle ex Ridsdale, *Blumea* 22: 546. 1975. *Franchetia sphaerantha* Baill., *Bull. Soc. Linn. Paris* 60: 477. 1885. TYPE: Madagascar. [Without exact locality], *Hildebrandt* 3309 (holotype, P!; isotypes, K!, L!).

Elattospermum longipetiolatum Soler., *Bull. Herb. Boissier* 1: 277. 1893. TYPE: Madagascar. [Without exact locality], *Hildebrandt* 3309 (holotype, L!; isotypes, K!, P!). Figure 2B.

Breonia parviflora Havil., *J. Linn. Soc. Bot.* 33: 37. 1897. TYPE: "Madagascar." [Without exact locality], *Hildebrandt* 3309 (holotype, K!; isotypes, L!, P!).

Shrubs to large trees, 7–18 m tall. Bark white-tinged, rugose. Leafy stems terete, puberulous to pubescent, lenticellate. Terminal vegetative buds, conical, $2-3 \times 1.2-1.5$ mm, puberulous. Leaves persistent; petioles $15-20 \times 0.9-1$ mm, terete, puberulous; blades $5.2-6.7 \times 2.5-3.9$ cm, elliptic to oblanceolate (oblong to oblanceolate), adaxially glabrous, abaxially puberulous, membranaceous, glossy, apex acuminate, base rounded to truncate;

margins glabrous, entire; secondary veins ca. 7 pairs per side, eucamptodromous, barely evident on upper surfaces, red-tinged when dry; domatia pocket-type in the axils of secondary veins, glabrous; stipules ca. 5×2 mm, cymbiform, not carinate, puberulous, free at the base, deciduous. Inflorescence solitary, heads 1–1.2 cm wide; inflorescence axes 2.4–3.8 cm long, usually bent and twisted when dry, terete, pubescent to velutinous; bracts calyptra-like, deciduous; peduncles ca. 1 mm long. Flowers mostly 4-merous or rarely 5-merous; calyx tubes ca. 1 mm long, green-yellow-tinged, inside velutinous, outside pubescent, lobes ca. 0.5 mm long, triangular, pubescent; corolla tubes $4.2-4.3 \times$ ca. 0.2 mm, yellow-tinged, glabrous, lobes ca. 1.2 mm long, elliptic, lower parts glabrous, toward the apex puberulous, ciliate; anthers ca. 1 mm long; filaments ca. 0.2 mm long, terete, glabrous; styles $6-7 \times$ ca. 0.8 mm, glabrous; stigmas globose to clavate; ovary 2-carpellate; carpels coherent; ovule 1 per locule, pendulous; placentae small, ovate. Infructescences 4–10 mm diam., densely pubescent, with well-developed calyx remnants; individual fruits with endocarp hard, glossy; disks accrescent, obconical; seeds 1 per locule, with one side convex, the other flattened, ellipsoid, red; seed-coat lineate.

Habitat and distribution. Lowland evergreen rainforests; Districts of Antsiranana II, Nosy Be, Ambanja, and Befandriana-Nord (Fig. 10).

Phenology. Flowering January–July; fruiting March–December.

Discussion. Baillon (1885), Solereder (1893), and Haviland (1897) all used different sheets of the same collection, *Hildebrandt* 3309, as the basis for *Franchetia sphaerantha*, *Elattospermum longipetiolatum*, and *Breonia parvifolia*, respectively. Neither Solereder nor Haviland knew about *Franchetia sphaerantha*, and Haviland did not cite *Elattospermum longipetiolatum* either.

Additional specimens examined. MADAGASCAR. **Antsiranana:** District Antsiranana II, Canton Anamakia, Ankotikona, 15273 SF (TEF); bords de rivière Kongony, Ambaliha, 2950 SF (TAN, TEF); District Nosy be, Lokobe Reserve, *Antilahimena* 82 (K, MO); Lokobe, 7822 RN (TAN), 9229 RN (TAN), 9453 RN (TEF), 11417 SF (TEF), 24764 SF (TEF); District Ambanja, *Randrianaivo* 255 (MO); Canton Marovato, Beangona, *Rakoto* 9 (TAN). **Mahajanga:** District Befandriana-Nord, Commune Tsarahonenana, Forêt domaniale d'Antetezana, 15947 SF (TEF); [unknown locality], 6257 RN (TEF).

17. *Breonia stipulata* Havil., *J. Linn. Soc. Bot.* 33: 35. 1897. TYPE: "Madagascar, Northwest" [without exact locality], 1841 (fr), *Pervillé* s.n. (holotype, P!).

recurved, with protuberance abaxially (Fig. 14E), glabrous, with a few scattered hairs at the apex, ciliate; anthers ca. 1.2 mm long; filaments 0.1–0.2 mm long; styles ca. 13×0.1 mm; stigmas clavate; ovary 2-carpellate; carpels syncarpous; ovules 4 to 5 per locule, flattened, imbricate; placentae elongated, strongly flattened. Infructescences 1.2–1.6 cm diam., with accrescent calyx remnants; individual fruits with endocarps soft, fibrous; disks accrescent, napiform; seeds 4 to 5 per locule, concavo-convex, ellipsoid, red; seed-coat reticulate.

Habitat and distribution. This species occurs in low- and mid-altitude evergreen rainforests; Districts of Nosy Be, Ambanja, and Maroantsetra (Fig. 12).

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Elattospermum longipetiolatum Soler., *Bull. Herb. Boissier* 1: 277. 1893. TYPE: Madagascar. [Without exact locality], *Hildebrandt* 3309 (holotype, L!; isotypes, K!, P!). Figure 2B.

Breonia parviflora Havil., *J. Linn. Soc. Bot.* 33: 37. 1897. TYPE: "Madagascar." [Without exact locality], *Hildebrandt* 3309 (holotype, K!; isotypes, L!, P!).

Shrubs to large trees, 7–18 m tall. Bark white-tinged, rugose. Leafy stems terete, puberulous to pubescent, lenticellate. Terminal vegetative buds, conical, $2\text{--}3 \times 1.2\text{--}1.5$ mm, puberulous. Leaves persistent; petioles $15\text{--}20 \times 0.9\text{--}1$ mm, terete, puberulous; blades $5.2\text{--}6.7 \times 2.5\text{--}3.9$ cm, elliptic to oblanceolate (oblong to oblanceolate), adaxially glabrous, abaxially puberulous, membranaceous, glossy, apex acuminate, base rounded to truncate;

margins glabrous, entire; secondary veins ca. 7 pairs per side, eucamptodromous, barely evident on upper surfaces, red-tinged when dry; domatia pocket-type in the axils of secondary veins, glabrous; stipules ca. 5×2 mm, cymbiform, not carinate, puberulous, free at the base, deciduous. Inflorescence solitary, heads 1–1.2 cm wide; inflorescence axes 2.4–3.8 cm long, usually bent and twisted when dry, terete, pubescent to velutinous; bracts calyptra-like, deciduous; peduncles ca. 1 mm long. Flowers mostly 4-merous or rarely 5-merous; calyx tubes ca. 1 mm long, green-yellow-tinged, inside velutinous, outside pubescent, lobes ca. 0.5 mm long, triangular, pubescent; corolla tubes $4.2\text{--}4.3 \times$ ca. 0.2 mm, yellow-tinged, glabrous, lobes ca. 1.2 mm long, elliptic, lower parts glabrous, toward the apex puberulous, ciliate; anthers ca. 1 mm long; filaments ca. 0.2 mm long, terete, glabrous; styles $6\text{--}7 \times$ ca. 0.8 mm, glabrous; stigmas globose to clavate; ovary 2-carpellate; carpels coherent; ovule 1 per locule, pendulous; placentae small, ovate. Infructescences 4–10 mm diam., densely pubescent, with well-developed calyx remnants; individual fruits with endocarp hard, glossy; disks accrescent, obconical; seeds 1 per locule, with one side convex, the other flattened, ellipsoid, red; seed-coat lineate.

Habitat and distribution. Lowland evergreen rainforests; Districts of Antsiranana II, Nosy Be, Ambanja, and Befandriana-Nord (Fig. 10).

Phenology. Flowering January–July; fruiting March–December.

Discussion. Baillon (1885), Solereder (1893), and Haviland (1897) all used different sheets of the same collection, *Hildebrandt* 3309, as the basis for *Franchetia sphaerantha*, *Elattospermum longipetiolatum*, and *Breonia parvifolia*, respectively. Neither Solereder nor Haviland knew about *Franchetia sphaerantha*, and Haviland did not cite *Elattospermum longipetiolatum* either.

Additional specimens examined. MADAGASCAR. **Antsiranana:** District Antsiranana II, Canton Anamakia, Ankotikona, 15273 SF (TEF); bords de rivière Kongony, Ambaliha, 2950 SF (TAN, TEF); District Nosy be, Lokobe Reserve, *Antilahimena* 82 (K, MO); Lokobe, 7822 RN (TAN), 9229 RN (TAN), 9453 RN (TEF), 11417 SF (TEF), 24764 SF (TEF); District Ambanja, *Randrianaivo* 255 (MO); Canton Marovato, Beangona, *Rakoto* 9 (TAN). **Mahajanga:** District Befandriana-Nord, Commune Tsarahonenana, Forêt domaniale d'Antetezana, 15947 SF (TEF); [unknown locality], 6257 RN (TEF).

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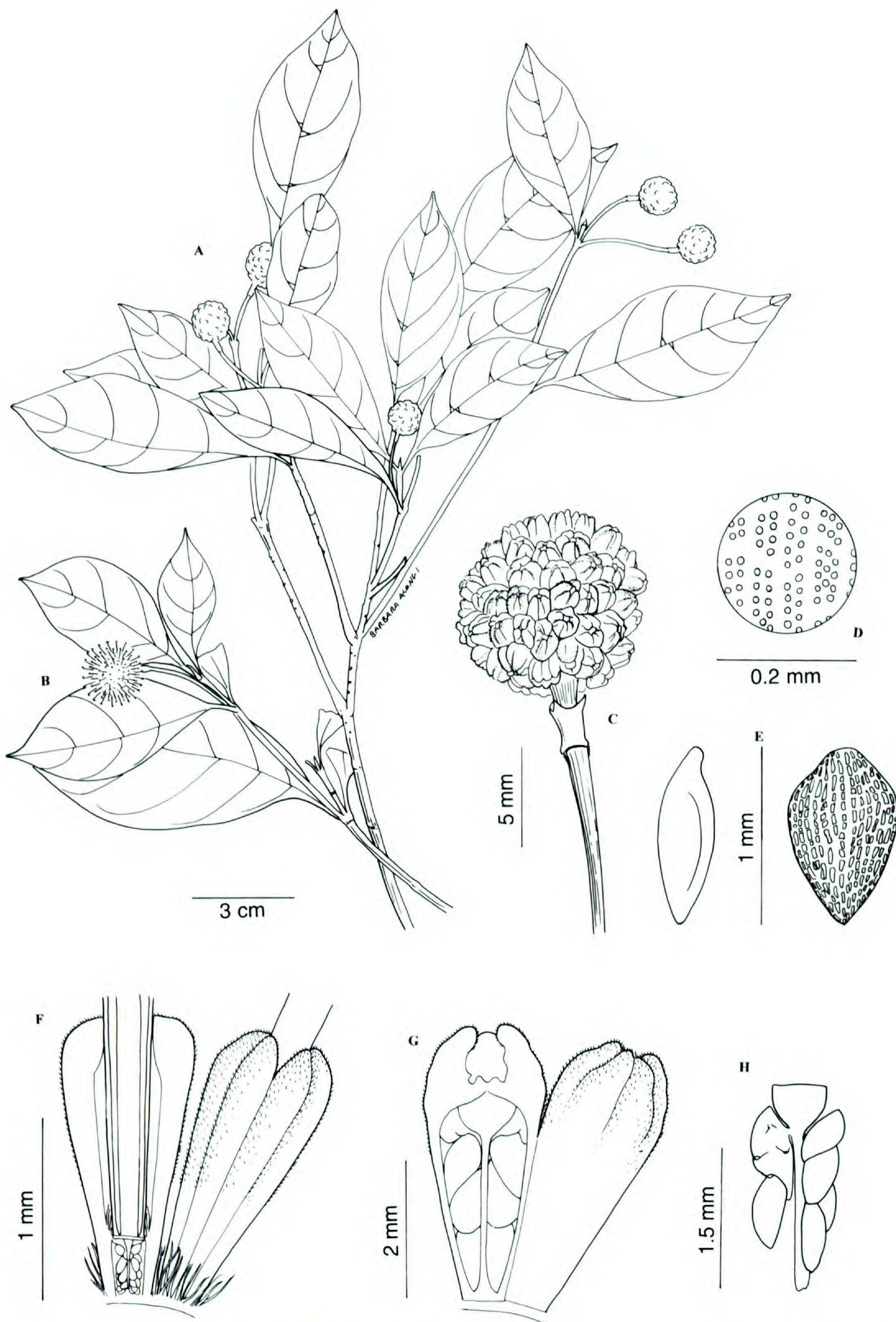


Figure 13. *Breonia richardsonii*.—A. Fertile branch with mature infructescences. —B. Fertile branch with inflorescence. —C. Mature infructescence, bearing a tubular bract. —D. Seed surface. —E. Seed, lateral view (left); dorsal

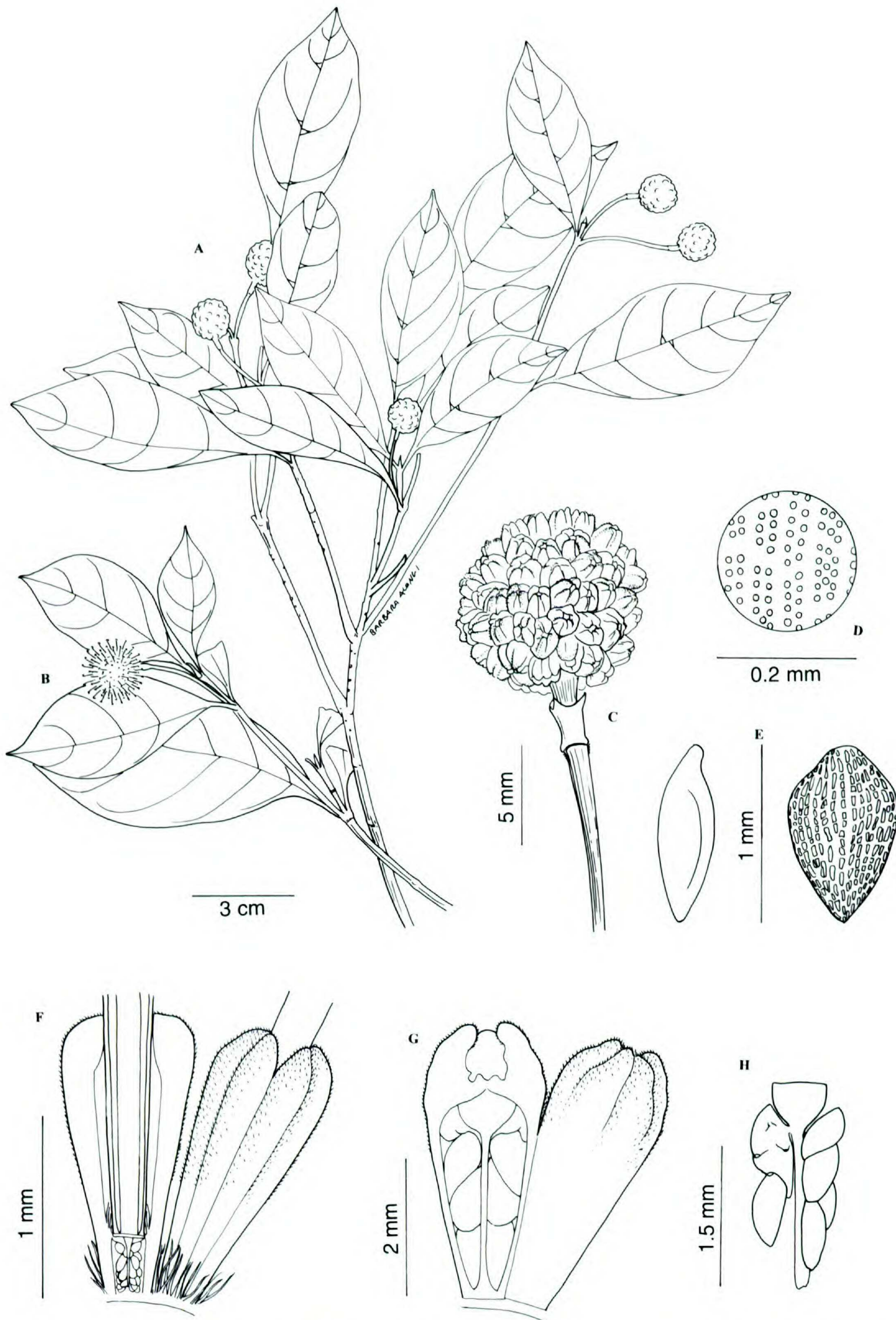


Figure 13. *Breonia richardsonii*.—A. Fertile branch with mature infructescences. —B. Fertile branch with inflorescence. —C. Mature infructescence, bearing a tubular bract. —D. Seed surface. —E. Seed, lateral view (left); dorsal

Trees or shrubs, 15–25 m tall. Bark rugose. Leafy stems quadrangular, glabrous. Terminal vegetative buds conical, 19–22 × 2–3 mm, glabrous. Leaves deciduous; petioles 12–22 × 1.5–2 mm, adaxially canaliculate, glabrous; blades 10–18.5 (–24.5) × 4.5–6 (–8) cm, elliptic to lanceolate, glabrous, coriaceous, not glossy, both apex and base acute; margins glabrous, entire; secondary veins (9–)11 or 12 pairs per side, eucamptodromous, abaxially prominulous; domatia absent (hairy or crypt-type domatia in the axils of secondary veins); stipules 15–18 × 2.2–2.5 (–3) mm, cymbiform, narrowly carinate abaxially, glabrous, free at the base, deciduous. Inflorescences solitary, heads 2.2–2.5 cm wide; inflorescence axes 4–6 cm long, strongly flattened, glabrous; bracts calyptra-like, deciduous; peduncles 1 mm long. Flowers 5-merous or rarely 4-merous; calyx tubes ca. 2 mm long, inside lanate, outside glabrous, toward the lobes puberulous, lobes ca. 1 mm long, oblong, tomentose; corolla tubes ca. 5 × 0.9–1 mm, glabrous, lobes 1.5–2 mm long, oblong, glabrous; anthers ca. 1.5 mm long; filaments 0.2–0.3 mm long; styles ca. 10 × 1 mm, glabrous; stigmas clavate to slightly cylindrical; ovary 2-carpellate; carpels syncarpous; ovules 1 to 2 per locule, pendulous, imbricate; placentae ovate, small. Infructescences 1.5–1.7 cm diam., with well-developed calyx remnants; individual fruits with endocarp hard, glossy; disks accrescent, heart-shaped; seeds 1 per locule, pendulous, concavo-convex, ellipsoid, both ends acute, red; seed-coat reticulate.

Habitat and distribution. Deciduous dry forests; Districts of Maintirano, Sambava, Andapa, Antsiranana II, and Antsalova (Fig. 10).

Common names. Valitsy and Vaomolompangady.

Phenology. Flowering October to December; fruiting December to February.

Additional specimens examined. MADAGASCAR. **Antsiranana:** District Andapa, Mandena, Forêt de Marojejy, *Rakotozafy & Raharilala 2189* (TAN); lisière de forêt, *Rakotozafy & Raharilala 2271* (TAN); trail to the summit of Marojejy Est, NW of Mandena, *Miller 3609* (K, MO, P, TAN); District Antsiranana II, Anivorano-Nord, Ambararamisakana, *15057 SF* (TEF). **Mahajanga:** District Antsalova, 1 km à l'Est de Bevitika, *Labat et al. 2263* (K, MO, P); Botomena, *11089 RN* (TEF); Tsiandro, Forêt d'Antsingy aux environs de la clairière de piste d'Ambodiriana, *6791 SF* (TEF), *12023 SF* (TEF), *18029 SF* (TEF); Forêt de Valoala, [collector unknown], *2200* (TAN).

18. *Breonia taolagnaroensis* Razafim., sp. nov.
TYPE: Madagascar. [Without exact locality], *Commerson s.n.* (holotype, P!). Figure 2F.

Haec species a congeneris disco nectarifero pentagono accrescente permagno distinguitur; ex sylvis littoralibus prope Taolagnaro tantum cognita.

Shrubs, 4–6 m tall. Bark rugose with annular fissures. Leafy stems quadrangular, glabrous. Terminal vegetative buds conical, 5–6 × ca. 3 mm, glabrous. Leaves persistent; petioles 13–20 × ca. 2.5 mm, adaxially canaliculate, glabrous; blades 9–11 (–16) × 3.5–6.5 cm, ovate to oblong, glabrous, coriaceous, glossy, apex rounded to broadly cuspidate, base cuneate; margins glabrous, entire; secondary veins (7–)9 to 10 pairs per side, eucamptodromous; domatia absent; stipules 6–10 mm long, cymbiform, not carinate, free at the base, glabrous, deciduous. Inflorescence not seen; inflorescence axes (4–)6–8.5 cm long, strongly flattened; bracts not seen; peduncles absent. Flowers not seen. Infructescences 1.5–2 cm diam., with well-developed calyx remnants; individual fruits with endocarp hard, glossy; disks accrescent, pentagonal; seed 1 per locule, concavo-convex, with rudimentary wings at both ends, red; seed-coat reticulate.

Habitat and distribution. Littoral forests and evergreen rainforests; Districts of Fort-Dauphin and Farafangana (Fig. 10).

Common names. Valotr'angady, Molompangady, and Marotsaka.

Phenology. Flowering unknown; fruiting October to December.

Discussion. Bosser (1984) argued that the type specimen of *Cephalidium citrifolium* (Poir.) A. Rich. is the *Commerson* collection on which I base *Breonia taolagnaroensis*. I disagree with Bosser because *Commerson s.n.* now in P has fruits only, but Richard used a specimen with both flower and fruit on which to base his *Cephalidium*. *Commerson s.n.* has a flower only and matches Poiret's original descriptions of his *Nauclea citrifolia*.

Breonia taolagnaroensis is distinguished from the other species of *Breonia* by its massive, accrescent pentagonal disks, and is known only from the littoral forests of the Taolagnaro (Fort-Dauphin) regions, thus the specific epithet. The type specimen of this

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view (right). —F. Median dissection through flower, showing bicarpellate ovary with numerous ovules (left); entire flower, showing part of corolla tube (right). —G. Dissection through a calyx remnant and a carpel of a separate fruit (left); entire individual fruit (right). —H. Naked carpel, showing an accrescent disk adnate to the septum and 5 ovules attached to the placentae. A–F from *14359 SF* (TEF) and G from *18311 SF* (TEF).

Trees or shrubs, 15–25 m tall. Bark rugose. Leafy stems quadrangular, glabrous. Terminal vegetative buds conical, 19–22 × 2–3 mm, glabrous. Leaves deciduous; petioles 12–22 × 1.5–2 mm, adaxially canaliculate, glabrous; blades 10–18.5 (–24.5) × 4.5–6 (–8) cm, elliptic to lanceolate, glabrous, coriaceous, not glossy, both apex and base acute; margins glabrous, entire; secondary veins (9–)11 or 12 pairs per side, eucamptodromous, abaxially prominulous; domatia absent (hairy or crypt-type domatia in the axils of secondary veins); stipules 15–18 × 2.2–2.5 (–3) mm, cymbiform, narrowly carinate abaxially, glabrous, free at the base, deciduous. Inflorescences solitary, heads 2.2–2.5 cm wide; inflorescence axes 4–6 cm long, strongly flattened, glabrous; bracts calyptra-like, deciduous; peduncles 1 mm long. Flowers 5-merous or rarely 4-merous; calyx tubes ca. 2 mm long, inside lanate, outside glabrous, toward the lobes puberulous, lobes ca. 1 mm long, oblong, tomentose; corolla tubes ca. 5 × 0.9–1 mm, glabrous, lobes 1.5–2 mm long, oblong, glabrous; anthers ca. 1.5 mm long; filaments 0.2–0.3 mm long; styles ca. 10 × 1 mm, glabrous; stigmas clavate to slightly cylindrical; ovary 2-carpellate; carpels syncarpous; ovules 1 to 2 per locule, pendulous, imbricate; placentae ovate, small. Infructescences 1.5–1.7 cm diam., with well-developed calyx remnants; individual fruits with endocarp hard, glossy; disks accrescent, heart-shaped; seeds 1 per locule, pendulous, concavo-convex, ellipsoid, both ends acute, red; seed-coat reticulate.

Habitat and distribution. Deciduous dry forests; Districts of Maintirano, Sambava, Andapa, Antsiranana II, and Antsalova (Fig. 10).

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18. *Breonia taolagnaroensis* Razafim., sp. nov.
TYPE: Madagascar. [Without exact locality], *Commerson s.n.* (holotype, P!). Figure 2F.

Haec species a congeneris disco nectarifero pentagono accrescente permagno distinguitur; ex sylvis littoralibus prope Taolagnaro tantum cognita.

Shrubs, 4–6 m tall. Bark rugose with annular fissures. Leafy stems quadrangular, glabrous. Terminal vegetative buds conical, 5–6 × ca. 3 mm, glabrous. Leaves persistent; petioles 13–20 × ca. 2.5 mm, adaxially canaliculate, glabrous; blades 9–11 (–16) × 3.5–6.5 cm, ovate to oblong, glabrous, coriaceous, glossy, apex rounded to broadly cuspidate, base cuneate; margins glabrous, entire; secondary veins (7–)9 to 10 pairs per side, eucamptodromous; domatia absent; stipules 6–10 mm long, cymbiform, not carinate, free at the base, glabrous, deciduous. Inflorescence not seen; inflorescence axes (4–)6–8.5 cm long, strongly flattened; bracts not seen; peduncles absent. Flowers not seen. Infructescences 1.5–2 cm diam., with well-developed calyx remnants; individual fruits with endocarp hard, glossy; disks accrescent, pentagonal; seed 1 per locule, concavo-convex, with rudimentary wings at both ends, red; seed-coat reticulate.

Habitat and distribution. Littoral forests and evergreen rainforests; Districts of Fort-Dauphin and Farafangana (Fig. 10).

Common names. Valotr'angady, Molompangady, and Marotsaka.

Phenology. Flowering unknown; fruiting October to December.

Discussion. Bosser (1984) argued that the type specimen of *Cephalidium citrifolium* (Poir.) A. Rich. is the *Commerson* collection on which I base *Breonia taolagnaroensis*. I disagree with Bosser because *Commerson s.n.* now in P has fruits only, but Richard used a specimen with both flower and fruit on which to base his *Cephalidium*. *Commerson s.n.* has a flower only and matches Poiret's original descriptions of his *Nauclea citrifolia*.

Breonia taolagnaroensis is distinguished from the other species of *Breonia* by its massive, accrescent pentagonal disks, and is known only from the littoral forests of the Taolagnaro (Fort-Dauphin) regions, thus the specific epithet. The type specimen of this

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view (right). —F. Median dissection through flower, showing bicarpellate ovary with numerous ovules (left); entire flower, showing part of corolla tube (right). —G. Dissection through a calyx remnant and a carpel of a separate fruit (left); entire individual fruit (right). —H. Naked carpel, showing an accrescent disk adnate to the septum and 5 ovules attached to the placentae. A–F from *14359 SF* (TEF) and G from *18311 SF* (TEF).

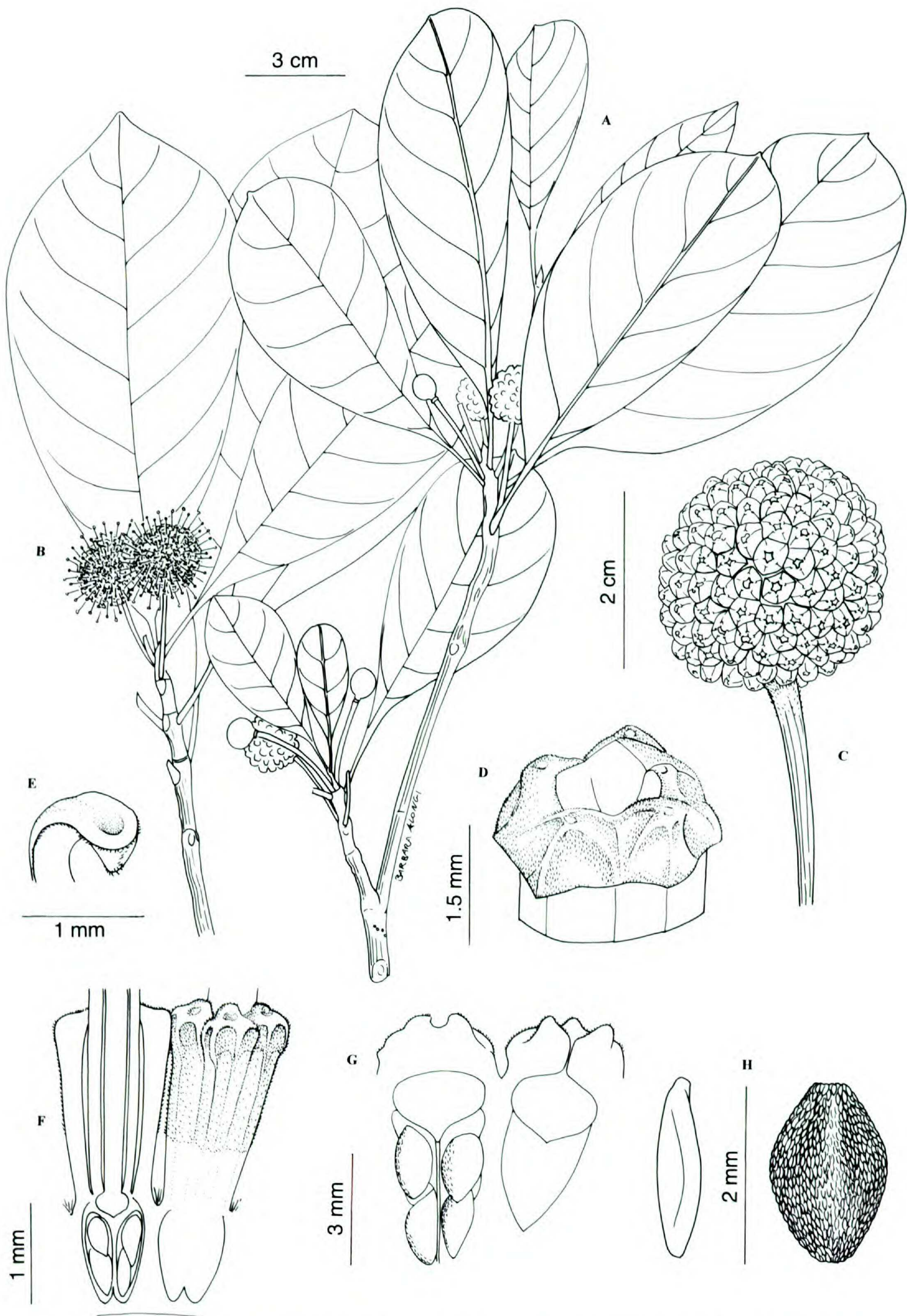


Figure 14. *Breonia sambiranensis*.—A. Fertile branch with infructescences. —B. Fertile branch with inflorescences. —C. Mature infructescence. —D. Calyx. —E. A corolla lobe bearing a protuberance. —F. Two adjacent flowers, showing two adjacent ovaries separated: median dissection through flower, showing a calyx and corolla tubes, and ovary (left);

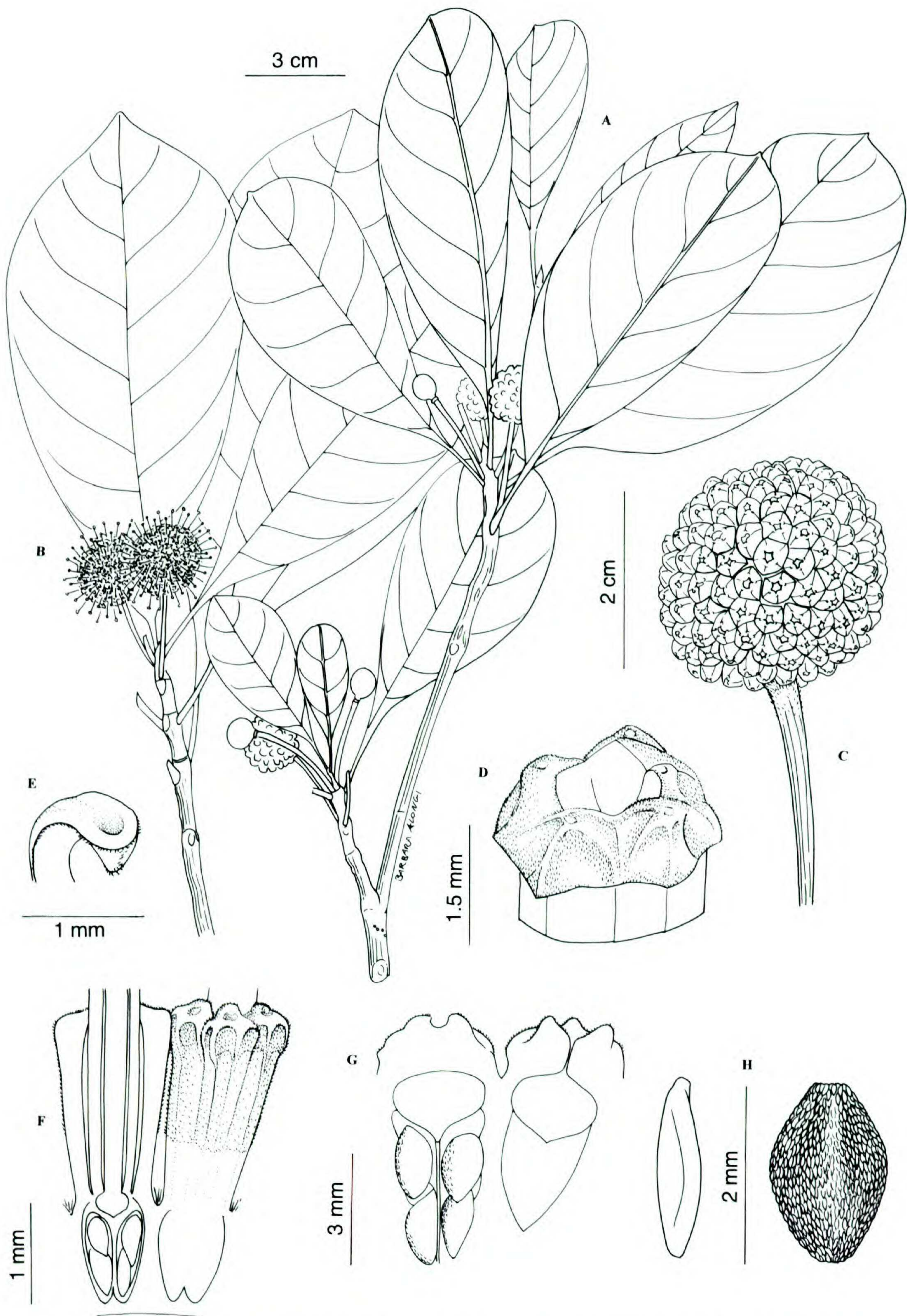


Figure 14. *Breonia sambiranensis*.—A. Fertile branch with infructescences. —B. Fertile branch with inflorescences. —C. Mature infructescence. —D. Calyx. —E. A corolla lobe bearing a protuberance. —F. Two adjacent flowers, showing two adjacent ovaries separated: median dissection through flower, showing a calyx and corolla tubes, and ovary (left);

species was identified by Capuron (1973b) as *Breonia chinensis* (Lam.) Capuron; however, it is distinguished from *B. chinensis* by having bark with annular fissures and by a single ovule per locule.

Paratypes. MADAGASCAR. **Fianarantsoa:** District Farafangana, Horombe, 4855 SF (TEF); Forêt de Manombo, 23641 SF (TEF). **Toliara:** District Fort-Dauphin, Forêt d'Analalava, Dumetz 1367 (K, MO); Forêt d'Ilandy au Nord de Fort-Dauphin, 20558 SF (TEF), McPherson 14391 (K, MO, TEF); Manantenina, Beharena, 10925 SF (TEF).

19. *Breonia tayloriana* Razafim., sp. nov.

TYPE: Madagascar. Toamasina: Fénériver Est, Tampolo, 3 Jan. 1956 (fl), 15703 SF (holotype, TEF). Figure 15.

Haec species a congeneris stipulis semipersistentibus amplis abaxialiter carinatis perfacile distinguitur.

Medium-sized trees, 9–10 m tall. Bark longitudinally fissured. Leafy stems quadrangular, lenticellate, glabrous. Terminal vegetative buds conical, 13–30 × 7–10 mm, glabrous. Leaves persistent, petioles 22–35 × 2–4.5 mm, adaxially canaliculate, glabrous; blades 18–32 × 10–15.5 cm, broadly obovate to broadly ovate, reddish, glabrous, coriaceous, glossy, apex obtuse to rounded, base cuneate; margins glabrous, entire; secondary veins 7 to 9 pairs per side, eucamptodromous, prominulous; without domatia; stipules 19–31 × 9–12.1 mm, cymbiform, abaxially carinate, glabrous, united at the base, semi-persistent. Inflorescences solitary (2 per axil), heads 3.2–3.5 cm wide; inflorescence axes 3.2–4.2 cm long, strongly flattened, glabrous; bracts calyptra-like, deciduous; peduncles 1–2 mm long. Flowers 5-merous; calyx tubes ca. 2 mm long, green, inside lanate, outside glabrous, lobes ca. 1.7 mm long, oblong to truncate, lanate; corolla tubes 8–9 × ca. 1 mm, light beige to cream, inside puberulous, outside glabrous, lobes ca. 1.8 mm long, oblong, at the lower parts glabrous, puberulous toward the apex; anthers ca. 1 mm long; filaments ca. 0.1 mm long, glabrous, terete; styles ca. 13 × 0.2 mm, glabrous; stigmas clavate; ovary 2-carpellate; carpels syncarpous; ovules 2 to 4 per locule, strongly flattened, pendulous, imbricate; placentae elongated. Infructescences 2–2.4 cm diam., with well-developed calyx remnants; individual fruits with endocarp soft, fibrous; disks accrescent, obconical; seeds 1 to 2 per locule strongly flattened, ellipsoid, red; seed-coat reticulate.

Habitat and distribution. Evergreen rainforests and littoral forests; Districts of Maroantsetra, Brickaville, and Fénériver Est (Fig. 10).

Common names. Molompangady mena (red lips of spade).

Phenology. Flowering December to February; fruiting February to April.

Discussion. The specific epithet honors Charlotte Taylor, a Rubiaceae specialist who has studied mostly the Neotropical Rubiaceae. Charlotte has taught me various aspects of taxonomy, including nomenclature, describing new species, writing a monograph, herbarium curation, and specimen annotation. The present revision was carried out under her supervision.

Paratypes. MADAGASCAR. **Toamasina:** District Fénériver-Est, Canton Ampasina, Itampolo, Zavah Paul 321-R-107 (TEF); District Brickaville, Ambila Lemaitso, Ampanotoamaizina, 8317 SF (TEF); District Maroantsetra, Masoala peninsula, coastal sand forest just N of Antalavia, Schatz et al. 1912 (K, MO, P, TAN); Jardin botanique de Farankaraina, 5652 SF (TEF), 63-R-199 (TEF); [Locality unknown], 32928 SF (TEF).

20. *Breonia tsaratananensis* Razafim., sp. nov.

TYPE: Madagascar. [Antsiranana province]: Massif de Tsaratanana, haut bassin de la Beandrarezina (Andranomena), affluent rive gauche de la Mahavavy, 2000–2300 m, 11 Nov. 1966 (fr), 27049 SF (holotype, TEF). Figure 16.

Haec species a congeneris tubo calycino supra medium dilatato apicem basemque constricto facile distinguitur.

Trees, 15–30 m tall. Leafy stems quadrangular, glabrous. Bark rugose. Terminal vegetative buds conical, 8–9 × ca. 3 mm, glabrous. Leaves persistent, petioles 15–20 mm long, adaxially canaliculate, glabrous; blades 9.5–11.3 × 5.2–6.5 cm, elliptic to obovate, glabrous, coriaceous, brittle when dry, glossy, apex mucronulate, base attenuate; margins glabrous, revolute, entire; secondary veins ca. 7 pairs per side, orange to yellow-tinged, eucamptodromous, prominulous; cryptic-type domatia at the base of the secondary veins, evident, ovate, glabrous; stipules ca. 10 × 3 mm, cymbiform, not carinate, glabrous, deciduous. Inflorescences solitary, heads ca 1.7 cm wide; inflorescence axes 2.5–3.3 cm long, slightly flattened, woody, densely pubescent; bracts calyptra-like, deciduous; peduncles ca. 1–2 mm long, densely pubescent. Flowers 5-merous or rarely

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entire flower (right). —G. Two adjacent fruits, showing two adjacent carpels separated: median dissection of mature infructescence, showing accrescent disk and seeds. —H. Seed, dorsal view (left); lateral view (right). A–F from *Antilahimena* 237 (MO) and G from 11407 SF (TEF).

species was identified by Capuron (1973b) as *Breonia chinensis* (Lam.) Capuron; however, it is distinguished from *B. chinensis* by having bark with annular fissures and by a single ovule per locule.

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TYPE: Madagascar. Toamasina: Fénériver Est, Tampolo, 3 Jan. 1956 (fl), 15703 *SF* (holotype, TEF). Figure 15.

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Haec species a congeneris tubo calycino supra medium dilatato apicem basemque constricto facile distinguitur.

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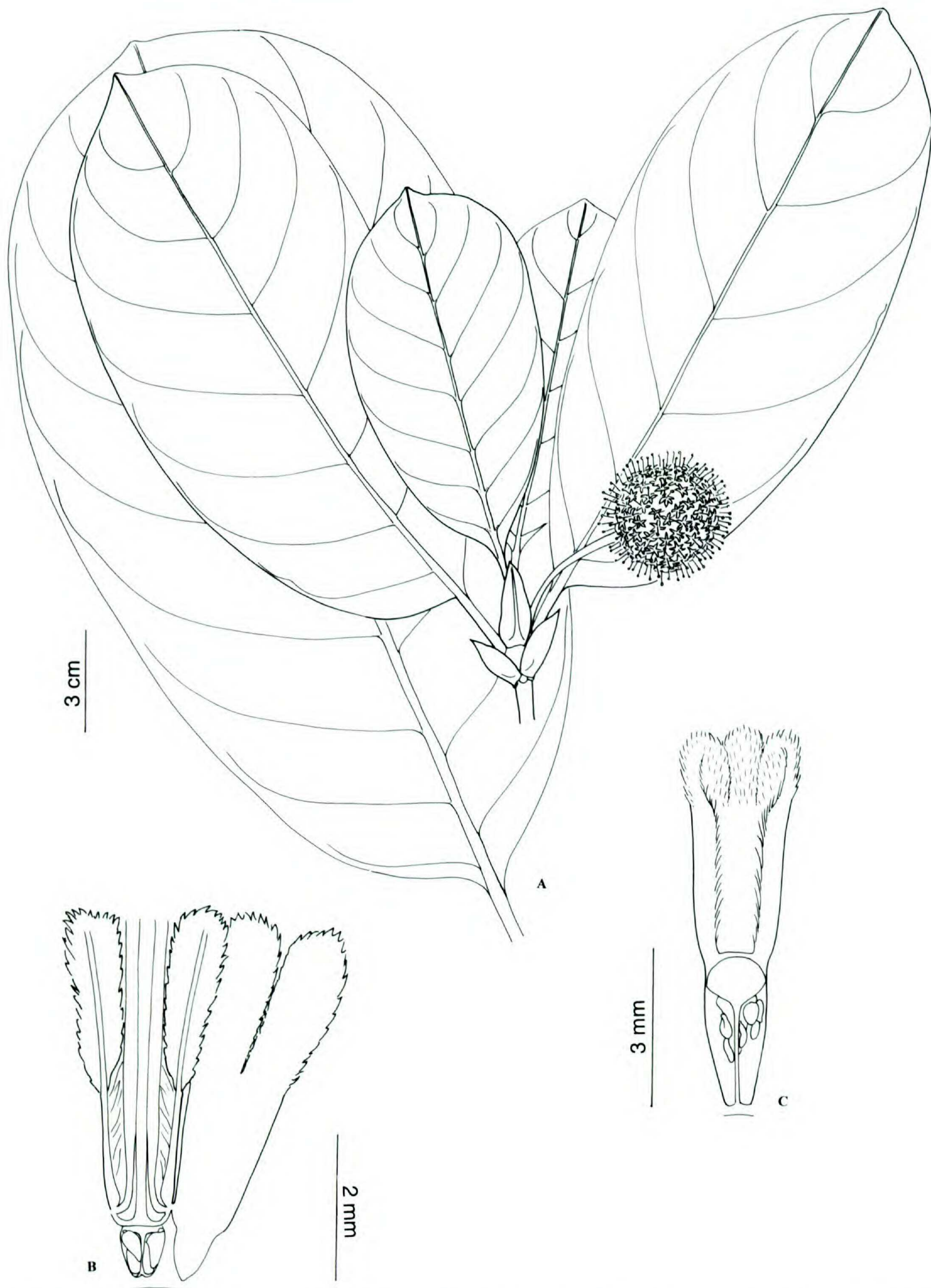


Figure 15. *Breonia tayloriana*.—A. Fertile branch with inflorescence and semi-persistent stipules. —B. Two adjacent flowers, showing two adjacent ovaries separated: median dissection through flower, showing lanate calyx and ovaries (left); entire flower (right). —C. Median dissection through a separate fruit, showing accrescent disk and ovaries with young seeds. A–C from 15703 SF (TEF).

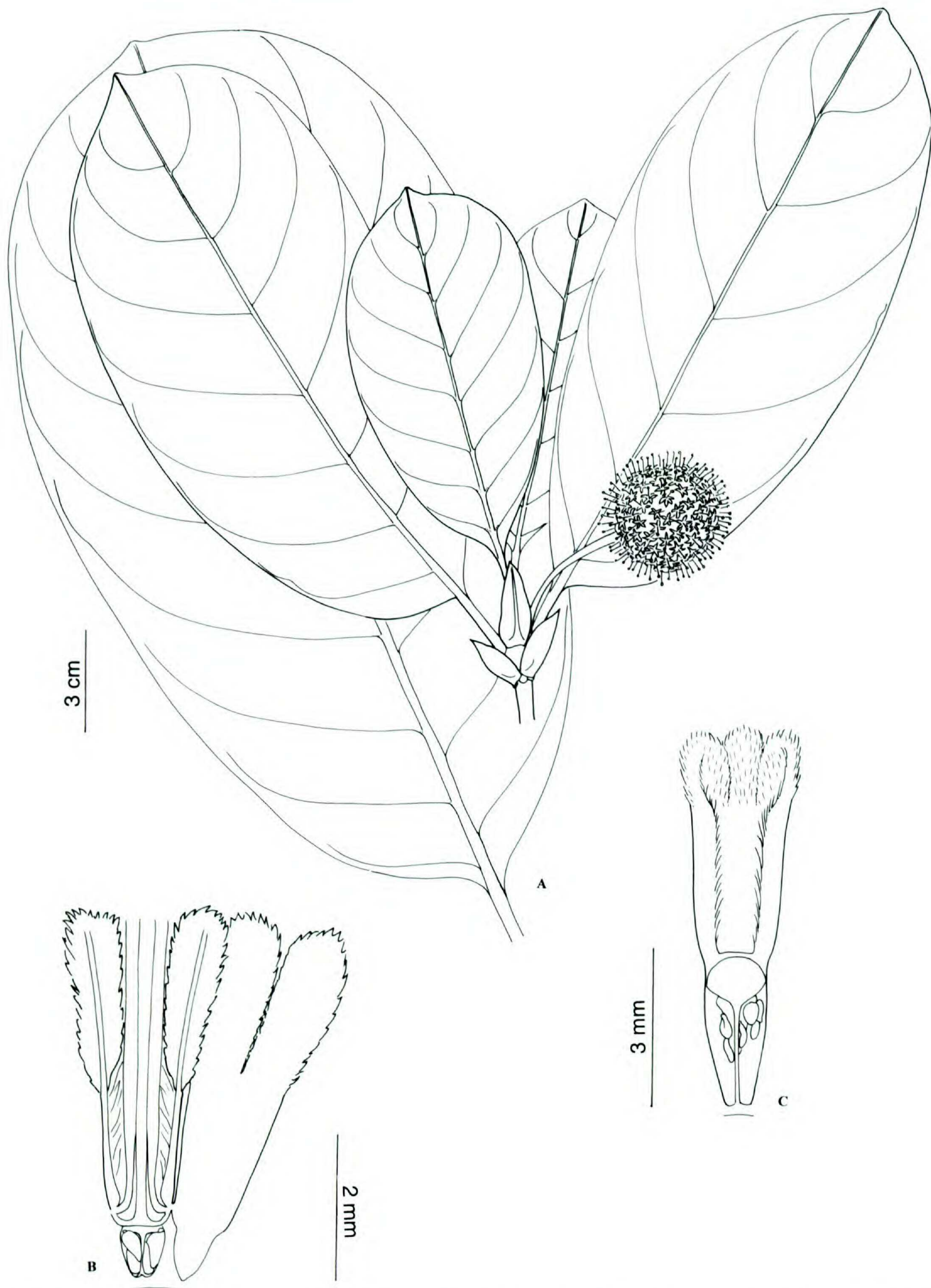


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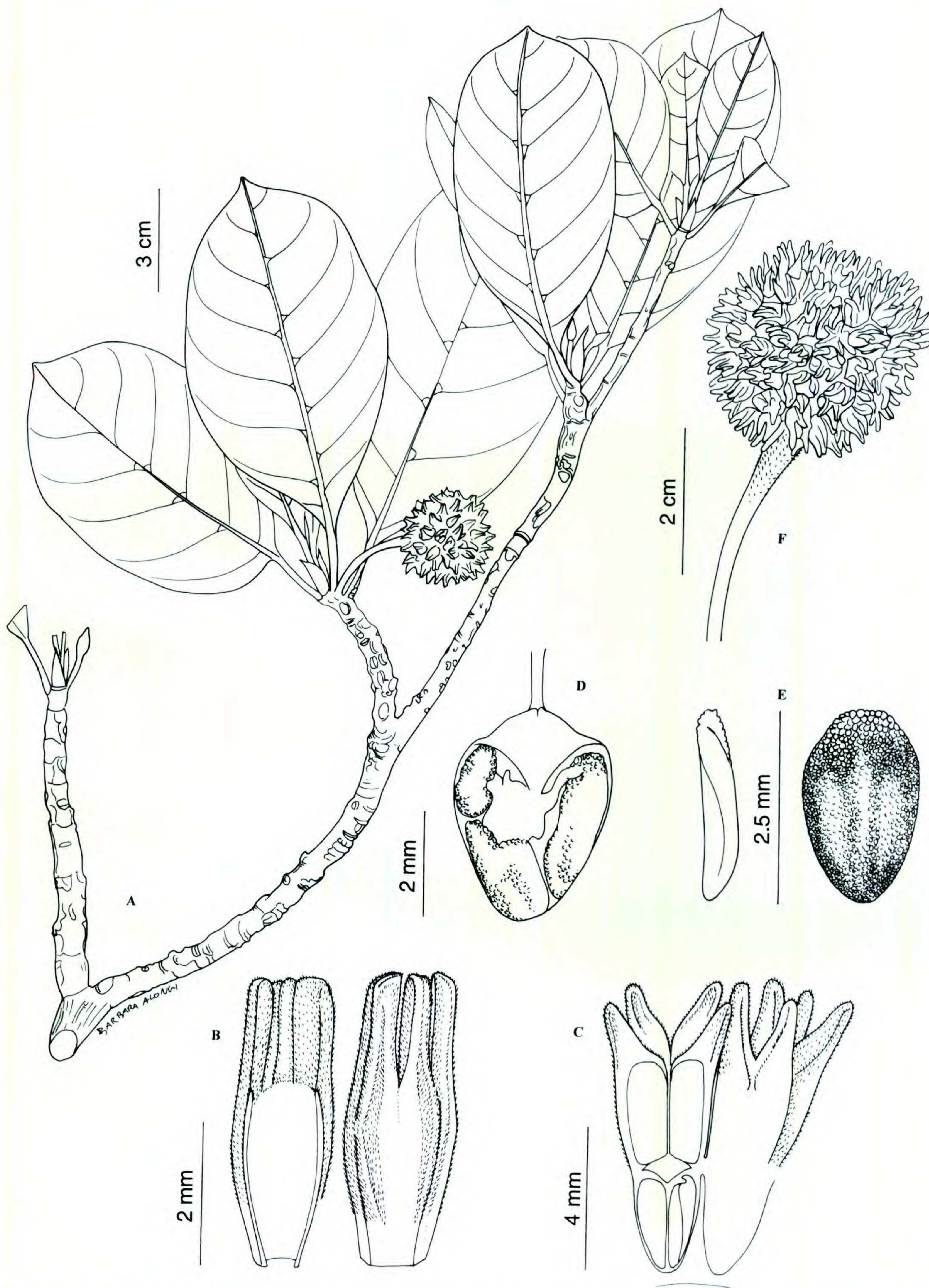


Figure 16. *Breonia tsaratananensis*.—A. Fertile branch with a young inflorescence and a mature infructescence. —B. Two adjacent flowers, showing two adjacent ovaries separated: median dissection of calyx with adaxial view (left); abaxial view (right). —C. Median dissection through fruit, showing accrescent disk and carpels with seeds (left); entire fruit (right). —D. Dissected unilocular ovary. —E. Mature seed: dorsal (left); lateral (right). —F. Mature infructescence. A, B from 973 SF (TEF) and C–F from 27049 SF (TEF).

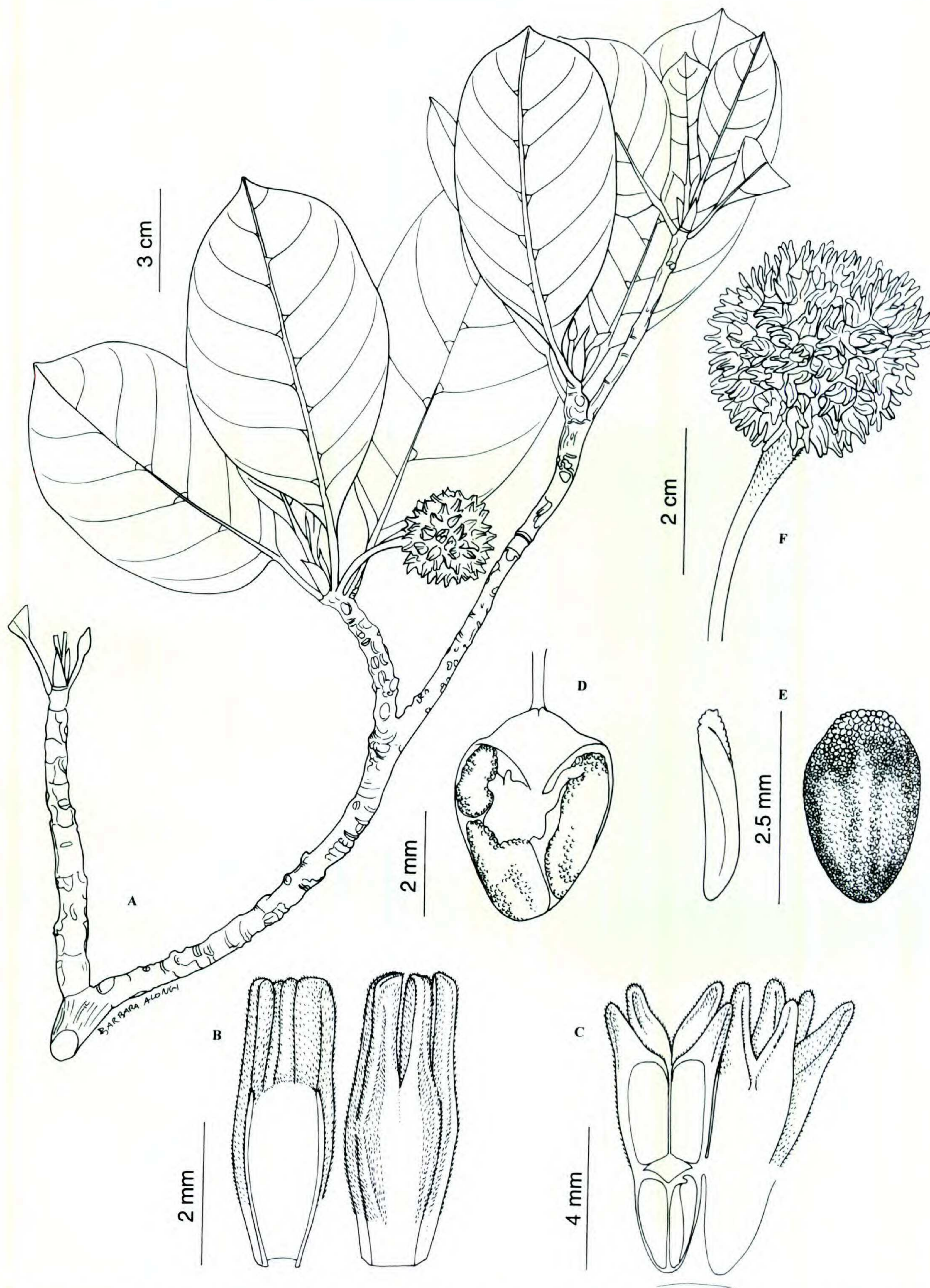


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4-merous; calyx tubes ca. 2.5 mm long, dilated above the middle, constricted at both ends, prominently ribbed, inside glabrous, outside puberulous, lobes truncate, ribbed, quadrangular, tomentose; corolla tubes 5–6 mm long, inside pubescent, outside puberulous; lobes ca. 2 mm long, recurved, puberulous; anthers not seen; style 7–8 mm long, glabrous; stigmas clavate; ovary 2-carpellate, rarely 1-carpellate; carpels syncarpous; ovules 3 to 5 per locule, pendulous, flattened, imbricate; placentae large, elongated. Infructescences 2–2.5 cm diam., with accrescent calyx remnants, persistent on the branches until the next flowering season; individual fruits with endocarp soft, fibrous; disks accrescent, triangular, seeds 3 to 4 per locule, concavo-convex, ellipsoid, dark red; seed-coat reticulate.

Habitat and distribution. Mid- and high-altitude humid forests; District Ambanja (including Tsaratanana Mountain) (Fig. 12).

Common name. Valotro.

Phenology. Flowering December to February; fruiting March to November.

Discussion. This species is known from five collections made from three individual trees; therefore, it is considered to be rare. Also, this is one of the two species of *Breonia* found only in high-altitude (above 1500 m) humid forests.

The specific epithet refers to the highest Malagasy mountain, Tsaratanana (2880 m), where the type species was collected.

Paratypes. MADAGASCAR. **Antsiranana:** District Ambanja, Massif de Tsaratanana, vallée de la Mahavavy, *Morat 2306* (MO, TAN). **Mahajanga:** Mangindrano, Ambohimirahavavy, *973 SF* (K, MO, TEF).

DUBIOUS SPECIES

Breonia longipetiolata Havil., J. Linn. Soc. Bot. 33: 36. 1897. TYPE: *Leprieur s.n.* (P!). This specimen, definitely belonging to *Breonia*, was reported to have been collected by Leprieur from French Guiana. However, the locality must be considered doubtful because *Breonia* is restricted to Madagascar and has never been reported from South America. Also, Leprieur never collected plants in Madagascar. The type and only specimen of *B. longipetiolata* does not match any of the species recognized here. This species is distinguished by its leaf blades with acute to rounded apices and long (ca. 9.6 cm) and strongly flattened peduncles.

EXCLUDED SPECIES

Breonia mayorii Setch. = *Sarcopygme mayorii* (Setch.) Setch. & Christoph. This species was orig-

inally placed in *Breonia* simply because of its multiple fruits. It has been transferred to the genus *Sarcopygme* of the tribe Morindeae based on the presence of raphides and bifid stigmas.

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4-merous; calyx tubes ca. 2.5 mm long, dilated above the middle, constricted at both ends, prominently ribbed, inside glabrous, outside puberulous, lobes truncate, ribbed, quadrangular, tomentose; corolla tubes 5–6 mm long, inside pubescent, outside puberulous; lobes ca. 2 mm long, recurved, puberulous; anthers not seen; style 7–8 mm long, glabrous; stigmas clavate; ovary 2-carpellate, rarely 1-carpellate; carpels syncarpous; ovules 3 to 5 per locule, pendulous, flattened, imbricate; placentae large, elongated. Infructescences 2–2.5 cm diam., with accrescent calyx remnants, persistent on the branches until the next flowering season; individual fruits with endocarp soft, fibrous; disks accrescent, triangular, seeds 3 to 4 per locule, concavo-convex, ellipsoid, dark red; seed-coat reticulate.

Habitat and distribution. Mid- and high-altitude humid forests; District Ambanja (including Tsaratanana Mountain) (Fig. 12).

Common name. Valotro.

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- Decary 5199 (5), 5511 (3), 5513 (3), 5573 (3); Dumetz 1367 (18).
- Gautier 3772 (2); Gautier et al. 3288 (6).
- Hildebrandt 3309 (16); Humblot s.n. (3).
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- Labat et al. 2261 (13), 2263 (17), Labat & Conté 2674 (13); Lewis et al. 755 (9); Louvel 125 (8), 186 (12), 216 (5).
- Malcomber 1219 (2), Malcomber et al. 1833 (13); McPherson 14391 (18); Miller 3609 (17); Morat 2306 (20).
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- Rabe 115 (15); Rahajasoja et al. 747 (3); Rakoto 9 (16); Rakotozafy & Raharilala 2189 (17), 2271 (17); Randrianaivo 247 (1), 251 (6), 255 (16); Randriamampionona 438 (6); Randrianasolo & Rasabotsy 32 (7); Ravelonarivo & Rabesaonina 570 (7); Razafimandimbison SG 257 (5), SG 273 (13), SG 352 (10), SG 358 (7), SG 389 (8); Réserves Naturelles: 2751 RN (1), 4905 RN (1), 5152 RN (6), 5524 RN (15), 6234 RN (1), 6257 RN (16), 6809 RN (6), 7822 RN (16), 7906 RN (2), 9002 RN (2), 9045 RN (6), 9052 RN (10), 9129 RN (10), 9229 RN (16), 9453 RN (16), 9982 RN (3), 11089 RN (17), 12975 RN (2).
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- Thouvenot s.n. (5), 91 (5), 117 (10); Turk et al. 643 (3).
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- Zavah 321-R-107 (19); 5524 RN (?).
- Unknown collectors: 12-R-B-172 (5); 14-B-R-230 (9); 86-R-118 (3); 63-R-199 (19); Herbar de la station agricole de l'Alaotra, 2200 (TAN).

APPENDIX I.

LIST OF SPECIES

1. *Breonia boivini* Havil.
2. *Breonia capuronii* Razafim.
3. *Breonia chinensis* (Lam.) Capuron
4. *Breonia cuspidata* (Baker) Havil.
5. *Breonia decaryana* Homolle
6. *Breonia fragifera* Capuron ex Razafim.
7. *Breonia havilandiana* Homolle
8. *Breonia louvelii* Homolle
9. *Breonia lowryi* Razafim.
10. *Breonia macrocarpa* Homolle
11. *Breonia madagascariensis* A. Rich.
12. *Breonia membranacea* Havil.
13. *Breonia perrieri* Homolle
14. *Breonia richardsonii* Razafim.
15. *Breonia sambiranensis* Razafim.
16. *Breonia sphaerantha* (Baill.) Homolle ex Ridsdale
17. *Breonia stipulata* Havil.
18. *Breonia taolagnaroensis* Razafim.
19. *Breonia tayloriana* Razafim.
20. *Breonia tsaratananensis* Razafim.

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Examined specimens are listed alphabetically by collector, followed by collection numbers; the species is indicated by a number in parentheses corresponding to the number in the List of Species.

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6. *Breonia fragifera* Capuron ex Razafim.
7. *Breonia havilandiana* Homolle
8. *Breonia louvelii* Homolle
9. *Breonia lowryi* Razafim.
10. *Breonia macrocarpa* Homolle
11. *Breonia madagascariensis* A. Rich.
12. *Breonia membranacea* Havil.
13. *Breonia perrieri* Homolle
14. *Breonia richardsonii* Razafim.
15. *Breonia sambiranensis* Razafim.
16. *Breonia sphaerantha* (Baill.) Homolle ex Ridsdale
17. *Breonia stipulata* Havil.
18. *Breonia taolagnaroensis* Razafim.
19. *Breonia tayloriana* Razafim.
20. *Breonia tsaratananensis* Razafim.

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Examined specimens are listed alphabetically by collector, followed by collection numbers; the species is indicated by a number in parentheses corresponding to the number in the List of Species.